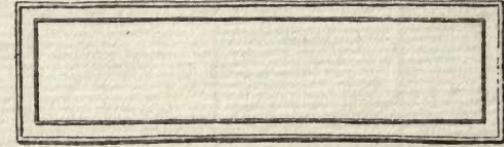
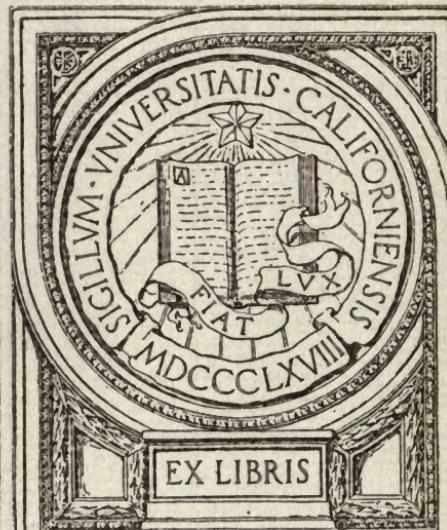
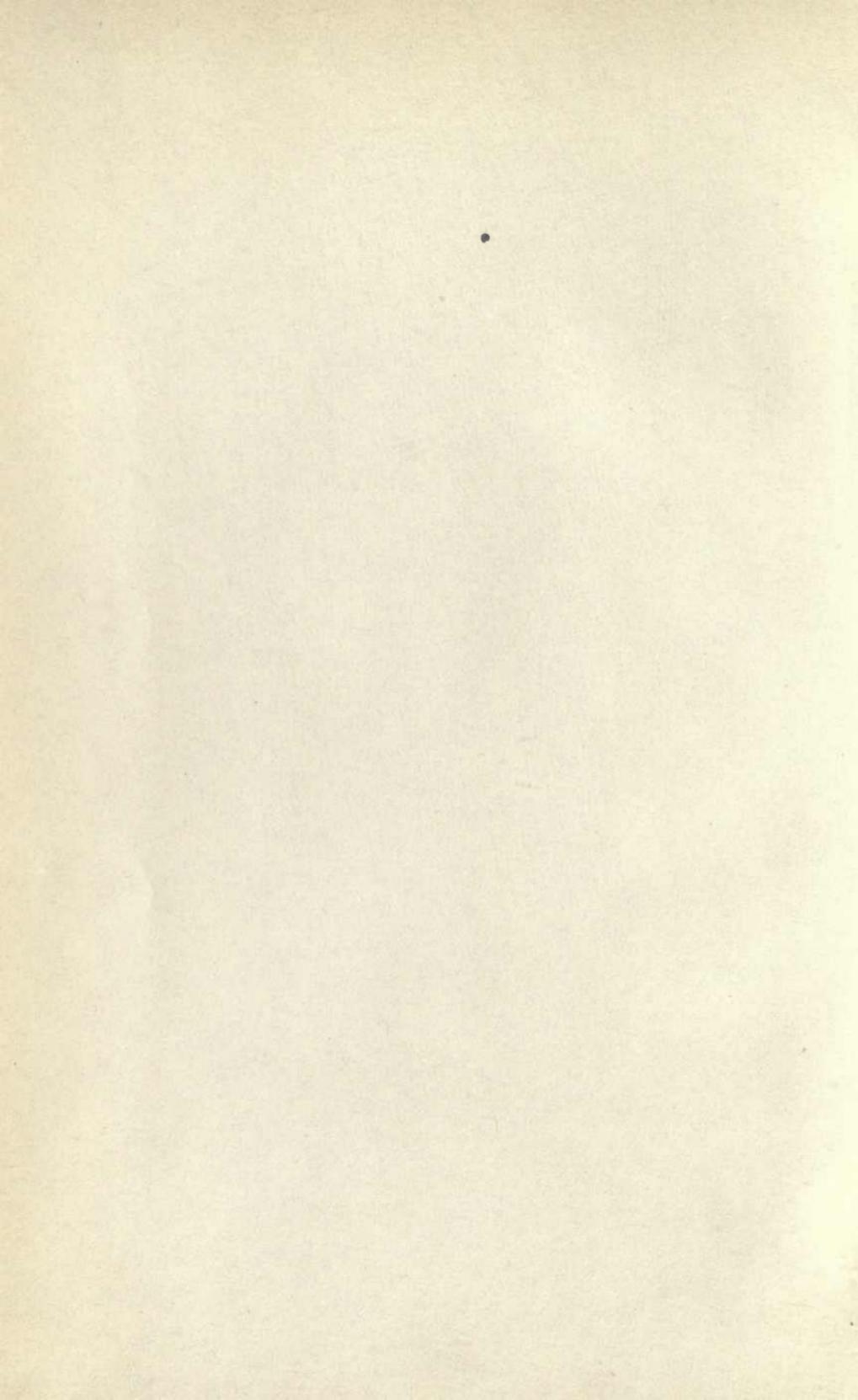


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[FIGS. I-81.]

DECEMBER 14, 1904.

STUDIES OF VARIATION IN INSECTS.

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THIS paper presents the results of certain qualitative and quantitative (statistical) studies of variation in a score of insect species. The individuals composing the various lots or series examined were taken from their natural habitat and nothing is known of the particular ancestry of any of them (except in the case of the bees). Nor is the environment (conditions of life) known more exactly than is commonly known of insects taken under such natural conditions.¹ The writers present quantitatively determined data which relate to (a) the distinction between congenital and acquired variation; (b) the distinction between continuous and discontinuous variation; (c) the existence of determinate variation; (d) tests of the rigor of natural selection; (e) the extent of congenital variation in parthenogenetically produced individuals compared with that in individuals of the same species, of bi-sexual parentage; (f) the extent of variation in males as compared with that in females of the same species; (g) correlated variation, especially in cases of bilateral symmetry and of metemerism; and (h) the significance of variation in the systematic study of insects. The paper is cast in such form that the specific data, tabulated and plotted, of the variations found in the various insect species studied follow a brief introductory part which refers to what seem to the writers the particular availability and worth of insects as subjects of

¹ For an account of variations in a single insect species among individuals of known ancestry and of known and experimentally controlled varying conditions of nutrition, see Kellogg and Bell, "Variations induced in larval, pupal and imaginal stages of *Bombyx mori* by controlled varying food supply," Science, V, 18, N. S., pp. 741-748, December, 1903.

variation studies. The specific data are finally followed by the general results, and the suggestions regarding the significance of the data and their application to various problems, arranged roughly according to certain particular phases or categories of variation.

INTRODUCTION.

Statistical and Quantitative Methods of the Study of Variation.—In the study of variation among certain insect species, the results of which are embodied in this paper, the authors have made constant use of the statistical and quantitative methods devised and explained by Galton, Pearson, *et al.*, and in this paper the graphic (frequency polygons and curves) and mathematical (standard deviation, coefficient of variability, etc.) expressions formulated and recommended by this school of biometric workers are used. The writers believe in the marked betterment and effectiveness of practically all variation study when pursued from the point of view of the biometrician, and they accept as a matter of course the formulæ and methods recommended by Pearson, *et al.*, for the mathematical expression of the status of variation.

But the danger referred to by the editors of *Biometrika* in their introductory editorial (vol. 1, 1901-1902, p. 5) is already apparent in the pursuit of the new science of variation. "The danger will no doubt arise," say the editors, "in this new branch of science that—exactly as in some branches of physics—mathematics may tend to diverge too widely from nature." Biologists are rarely mathematicians, and only mathematicians can understand the results and the worth, or even the purport, of some of the recent biometric papers.

From the writers' point of view the study of variation is a phase of biology, and not of mathematics. Its basic data are biological and not mathematical; they lack, even at best, the definitiveness and absoluteness of purely mathematical data, and the superstructure of mathematical development and the expression of facts and principles based on these data, which characterize the papers of the extremest biometricians, seem insecure in their foundations. The methods which produce these expressions seem over-refined, and carried to an extreme made unten-

able by the existence of the large personal equation and probability of error elements in the methods necessarily employed in the collection of the foundation data. However this may be — and the authors are not mathematicians enough fairly, perhaps, to venture such an opinion — it is certain that these extremer biometrical papers not only fail to attract or interest biologists, but repel them. And if mathematics is to revolutionize biological inquiry or even to help it effectively it must keep within hailing distance of the working biologists.

In this paper mathematical expressions are used wherever they are necessary or seem helpfully usable, but they are not used where they seem unnecessary or their appearance of accuracy and quantitative exactness seems delusive because of the character of the data on which they have to be based.

Further, the writers believe that certain variations are more advantageously and valuably expressed qualitatively than quantitatively. For these qualitative variations the mathematical treatment may well stop with the erection of the frequency polygons, which are always of unquestioned value both as graphic and as quantitative expressions of the range and frequency found in any statistical study of variation. Such variations as difference in color, in pattern, in character of venation, etc., are considered by the authors as qualitative variations (substantive of Bateson) as contrasted with dimensions, and the number of spines, spurs, segments, etc. (Bateson's meristic variations), which lend themselves especially to thorough-going quantitative treatment.

Insects Specially Advantageous Subjects for Variation Studies. — That the insects offer special opportunities for the study of variation is readily apparent when a few facts concerning them are recalled. First to be noted is the overwhelming dominance in number of species of this class of animals as compared with the species total in other classes; quite two-thirds of all the known species of living animals are insects. These animals, too, are unusually prolific; multiplication proceeds by a high ratio, and the life cycle is usually short. This results in many species being represented by uncountable hosts of individuals; recall the Rocky Mountain locust, the chinch bug,

Fitch's estimate of twelve million cherry aphids to the tree in a badly infested orchard, and Doten's ground-covering armies of western crickets in eastern Nevada, with two miles of rank front and a thousand yards of file depth. Yet with all this numerical wealth of kinds and individuals, insects show an amazing steadfastness of fundamental structural plan and a striking consistency of physiological processes. This brings it about that insects compete sharply with one another in the struggle for place and food. At the same time the abundance of individuals insures a wealth of small variations, and an increased chance for larger variations, *i. e.*, "sports." Thus Natural Selection ought to find a congenial field in the insect class, its two prerequisites, (*a*) numerical and heterogenic wealth of variations, and (*b*) sharp competition, coexisting and strongly emphasized. On the practical grounds, too, of ease of collecting, preserving, and studying large series of individuals, of accurate determination of geographic limits, and of the possession by the subjects of distinctive substantive characters, such as strongly colored, sharply delineated pattern, as well as readily counted or measured meristic characters, as tarsal and antennal segments, spines, hooks, hairs, etc., the insects are peculiarly advantageous subjects for variation studies. Finally, many insect species with quickly succeeding generations may be readily bred, generation after generation, in the vivarium or laboratory, under practically natural conditions, or under conditions of controlled varying nutrition, temperature, light, humidity, etc., thus affording opportunity for studies in heredity and for experimental studies demanding accurately determined controlled changes in conditions of life.

But most important recommendation of all is the fact that the unique character of the post-embryonic development obtaining among the more specialized orders of insects affords an opportunity to distinguish sharply between variations which must be held to be strictly blastogenic (congenital) and others which may be in large part acquired. The immense desirability of being able to distinguish between strictly congenital and acquired variations is of course obvious to all students of variation, heredity and species-forming. If acquired characters (acquired

variations) are not directly heritable, the only variations which give Natural Selection its validity as a species-forming factor are the congenital ones. If the relation of variation to species-forming is to be studied, the congenital variations, clearly apart from those adaptively acquired during the development of the individual in response to the immediate influence of the conditions of life, are the only ones that neo-Darwinians can consistently take into account. The great majority of published variation studies have apparently, however, left this distinction between blastogenic and acquired variations wholly out of account, with results that seem to us to invalidate seriously the application of the generalizations arrived at to the problem of species-forming, granting for the argument the truth of what is believed to be true by apparently the majority of working naturalists, namely, the non-heritability of acquired characters.

As this matter of the importance of distinguishing between congenital and acquired variations is referred to again in some detail at the beginning of the next section of this paper, its discussion may be left now for the presentation of a brief account of those conditions in insect-development which we believe afford a criterion for making the distinction between the two sorts of characters in the case of the variations presented by the fully developed imagines (adults) of insects with complete metamorphosis.

Character of Development of Specialized Insects Affording Means of Distinguishing Between Blastogenic and Acquired Variation.—Without by any means exhausting the subject of the post-embryonic development of insects, entomologists have become sufficiently well acquainted with the phenomena attending this development to be able to confirm absolutely (in essential character) Weismann's discoveries in the larva of the "imaginal discs" as the independent embryonic centers from which develop the wings, legs, antennæ and some other parts of the winged imagines (adults) of insects with complete metamorphosis. That is to say, in all the insects which hatch from the egg in a larval condition markedly different from the definitive condition of the species in its fully developed, mature stage, many of the adult organs, as, conspicuously, the external parts

of the head, and the legs and wings, are produced not by a gradual development, growth and transformation of the corresponding larval parts, but by a special development in late larval life and during the pupal stage (the beginnings may appear in early larval or even embryonic life) from small groups of previously undifferentiated subembryonic cells, derived in the case of the external parts just named chiefly from invaginations of the larval cellular skin-layer. In the larva (maggot) of a house-fly, for example, there are no functional legs or wings; there are no external signs (buds, pads) of these organs at any time in the larval stage. In all the larval life there can be no possible moulding influence on these future adult organs of the nature of any direct response or reaction to the immediate environment which we might assume possible if the wings and legs were slowly transforming external structures subject to attempts at or actual functional use in flight or crawling during the larval life. At pupation the wings and legs suddenly appear as external parts, but still equally functionless, and now wholly concealed and protected by the opaque chitinized wall of the puparium. With the final issuance of the adult the wings and legs appear for the first time in functional condition, and with the simple need of unfolding, expanding and drying the outer wall, an operation requiring but few moments, they appear at this time in their definitive fully developed condition. The wings have the arrangement of veins and number of spines and fringing hairs, the legs have the armature of spines and spurs and number of segments which they retain unchanged through the short or longer adult life. The imaginal wings and legs of all insects with complete metamorphosis—and the insects of this category include the beetles (Coleoptera), two-winged flies (Diptera), moths and butterflies (Lepidoptera), ants, bees, wasps, gall flies and ichneumons (Hymenoptera) and some other orders—are exposed during their development to just one set of extrinsic influences, namely, those of nutrition, temperature, humidity, etc. These influences affect the whole body and metabolism of the developing insect, but have no specific relation to specific parts, as exemplified by the relation of opportunity for use or disuse on the part of locomotory or sensory organs (wings, legs,

antennæ, eyes, auditory organs) to the habits of the insect, of the size or shape or number of special parts to direct needs on their part of adaptation to environing conditions, and by other such relations between the conditions of life and the developing organism.

An important one of these special environing conditions of life, and one that certainly works direct and apparent influence on the body wall of certain animals, is what may be called the chromatic condition of the environment. Color and pattern adapted to the needs of protection or aggression are phenomena familiar throughout the animal series. Most of such color and pattern conditions, catalogued under the heads of protective resemblance, mimicry, warning colors, etc., are fixed conditions as far as the individual is concerned, presumably brought about by the age-long action of natural selection. But not a few animals display the capability of achieving marked adaptive changes, *i. e.*, acquired variations, during their immature life (post-embryonic development). It is obvious that insects of complete metamorphosis, which possess in adult stage a color scheme and pattern wholly different from that of the larva or pupa and one which is not apparent until it appears in fixed definitive condition on the emergence (and drying) of the imago from the pupal cuticle, cannot be conceived to show, in their color-pattern, variations due to individual adaptive changes. That is, variations in this color-pattern among the individuals of a species are not acquired (except in so far as they are produced by the general influences of nutrition, temperature, etc., working without reference to the external chromatic conditions of the environment) but are strictly congenital.

Even such all-pervading influences as nutrition, temperature, humidity and light may be, and in many cases obviously are, so nearly practically identical for all the members of one brood or even for all the individuals of the species, that they can have little or no influence in causing variations. For conspicuous example the case of the honey bee may be noted. Here all the larvæ live side by side under identical conditions (those of the hive) of temperature, humidity and light, and the distribution of exactly similar food to them in similar quantity is probably as

nearly exactly uniform as could be guaranteed under our most careful artificial (experimental) conditions. The pupæ are, as well, under identical conditions of temperature, moisture and light, so that when the adults issue the variations to be found in any of their parts may with complete confidence be ascribed to prenatal influences, to intrinsic causes. They are purely blastogenic. Similarly, the conditions of life of the developing individuals of all the other social insects, the termites, ants and social wasps, are practically identical.

With the insects with incomplete metamorphosis, as the Orthoptera, Hemiptera, Corrodentia, *et al.* (that is, those which hatch from the egg in the general guise of the adult, although always wingless and of minute size) the appendages of the head (mouth parts and antennæ), as well as the eyes and general head wall and also the legs and external genitalia, are the same organs as the corresponding adult ones; whatever developmental changes take place are of the nature of a gradual modification from immature to definitive imaginal condition. The wings however, are never functional until after the final moulting (the one just prior to the assumption of the complete imaginal condition of the whole body) and so are probably not capable of modification (adaptive variation) due to use or disuse or to any direct special influence of the environment. Variations in wing characters of adult individuals of any insect species of incomplete metamorphosis ought therefore to be strictly congenital (other than differences, as of size, perhaps, due to the influence of nutrition, humidity, temperature, and light). But such characters as the color and pattern of the body-wall might very well be modified by the direct influence of the environment. For example with certain genera of locusts, as *Trimerotropis*, *Spharagemon*, *et al.*, there are marked individual variations in coloration and pattern, obviously adaptive for the sake of protective resemblance. It may well happen that the individuals of a single brood starting life of similar color and pattern should acquire varying protective coloration modifications, if such requirement be actually possible. We know from the experiments of Poulton and others that the body-wall of certain insects, particularly the larvæ of *Papilio* butterflies, can respond directly

to the influence of the chromatic environment (larvæ nearing pupation acquire variously colored pupal cuticle depending directly on the color of the immediate environment at the time of pupation). The legs, antennæ and mouth parts of insects with incomplete metamorphosis may be influenced by use or disuse, and perhaps in other direct ways, during the immature life (post-embryonic development) of the individuals. These insects have an exposed immature life like that of most other animals and the variations apparent in their adult structures may be and almost certainly are, in the case of certain characters partly adaptive, *i. e.*, acquired. In this they differ, *as also do almost all other animals*, from the insects with complete metamorphosis, of which we may say confidently that the variations exhibited by the adults in the case of numerous parts, especially the wings, legs, antennæ, mouth parts, eyes and the spines, hairs and other processes of the body-wall as well as the pattern and color of the body-wall, cannot possibly be regarded as adaptive, *i. e.*, acquired, but must be held to be strictly blastogenic.

SPECIFIC DATA OF VARIATIONS IN VARIOUS INSECTS.

Variation in Venation and Number of Hooks in *Apis mellifica* (the honey bee).¹—The honey bee, *Apis mellifica*, is an insect with complete metamorphosis. The larvæ are footless, soft-bodied, white grubs which are born from eggs laid in the cells, and which live for their whole life protected and cared for in cells, those of any one community under identical conditions of light and temperature and presumably of food and care. Even those of different communities have practically an identi-

¹ Since the present account of our observations of the variation in the wings of drones and worker honey bees was finished and made ready for the printer a paper entitled "Comparative Variability of Drones and Workers of the Honey Bee," by D. B. Casteel and E. F. Phillips has been published (*Biol. Bull.*, Vol. VI, December, 1903, pp. 18-37). It is of interest to compare the results thus independently obtained by two pairs of observers. The general conclusion in both cases is the same, viz., that the drones (parthenogenetically produced) vary more than the workers (bisexually produced). In the absence of experimental proof, the present writers are hardly willing to recognize the large importance which Messrs. Casteel and Phillips give to extrinsic factors (depending on the shape and size of the brood cells) in producing the drone variation.

cal environment. The larvæ pupate in the cells, and the imaginal bees issue with wings, legs and numerous other structures wholly formed and in definitive character, and not corresponding to any functional larval parts. The variations therefore in the wings,—to select structures particularly available for quantitative comparison, and wholly foreign to the larval body as functional parts, *i. e.*, parts capable of use or subject to disuse,—must be looked on as variations as strictly congenital and independent of modifying extrinsic influence (*i. e.*, without trace of modifications acquired during development due to varying environment) as it is possible to find among animals. The wings, also, are structures possessed by all the three kinds of individuals composing the honey-bee species, and in all three kinds function identically so that any variations the wings may exhibit can not be attributed to differences in the special function of the wings in the different kinds of individuals, but may be safely associated with the other general features in the make-up of each kind of individual, and be referred to as fair indicators of the kind and extent of variation characteristic of the different kinds of individuals.

These variations, thanks to the uniquely favorable circumstances of the honey bee's domestic economy, may be studied in series of individuals of adult age and experience, which have been exposed (in their work of nectar, pollen and propolis gathering, etc.) to the dangers of birds, lizards, predaceous insects, storm and general stress of external physical conditions, and in series of adults just issued or ready to issue from the cells, and thus not yet exposed in any way in adult winged condition to the selective struggle for existence. The variations also may be compared in series of males (drones) and series of females (workers),¹ and also in series of parthenogenetically produced individuals (drones) and of individuals of bisexual parent-

¹ Workers should never be regarded as neuters, that is sexless individuals. All workers possess, in rudimentary but not always functionless condition, ovaries composed of several egg-tubes, oviduct and rudimentary spermatheca; so-called fertile workers, *i. e.*, workers capable of producing and laying (unfertilized) eggs are not infrequent. These eggs are of course unfertilized, these fertile workers never mating. The eggs laid by fertile workers produce only drones.

age (workers). Also series of the progeny of a single mother (queen) may be compared with a series of individuals representing several different mothers (queens). Altogether the honey bee is an animal species of unusual availability and worth to the student of variation.

Variations in Character of Venation.—A lot of 300 drones from our laboratory hive (Italians) was examined for variations in the character of the venation. (The wings were removed and mounted on glass slides).

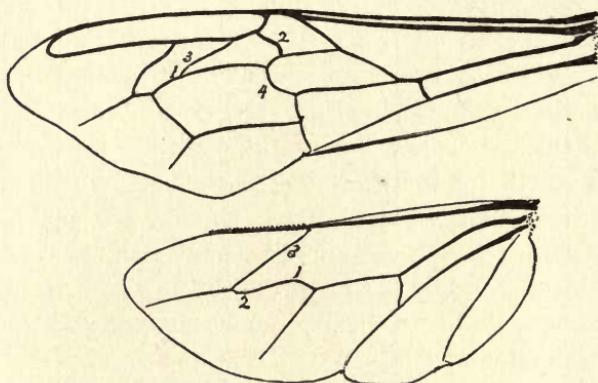


FIG. 1. Fore and hind wings of honey bee (drone) showing normal venation; points where variation may occur indicated by numbers.

The normal venation of the front wings is shown in figure 1. The variations observed in the fore wing consist of the complete or partial absence of the little cross vein at point 1 characterized as "var. 1 complete," and "var. 1 incomplete," and of the addition of a spur at points 2, 3 to 4, characterized as "var. 2," "var. 3," and "var. 4" "slight" or "very slight" depending on length of the spur; and of the interpolation of a complete or almost complete new cell in the discal region of the wing, characterized (and in each case figured) as "complete new cell" and "almost complete new cell." (See Figs. 2-5 for illustration of these variations.)

Of the 300 left fore wings, 22 were torn; of the remaining 278: 100 show no variation (fig. 1); 77 show var. 2, var. 3 or var. 4, in either very slight, slight, "fair," "good" or "marked" degree or two or three of these variations in combi-

nation (figs. 2 and 3); 84 show var. 1 complete (fig. 3); 13 show var. 1 incomplete (fig. 2); 2 show an almost complete new

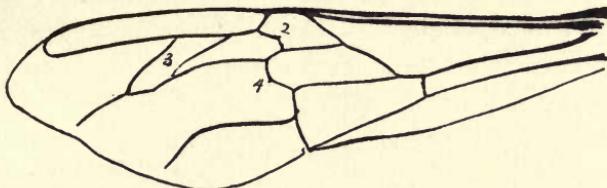


FIG. 2. Fore wing of honey bee (drone) showing var. 1 incomplete, and small spurs at 2, 3 and 4.

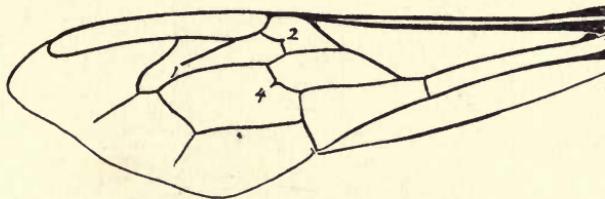


FIG. 3. Fore wing of honey bee (drone) showing var. 1 complete, and good spurs at 2, 3 and 4. (Spur and number at 3 unfortunately omitted in the figure.)

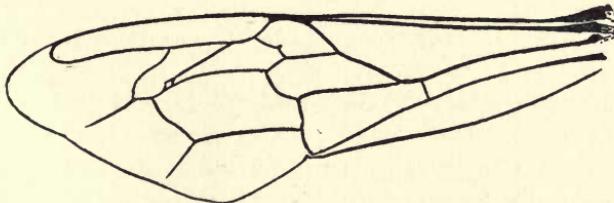


FIG. 4. Fore wing of honey bee (drone) showing almost complete cell at 1.

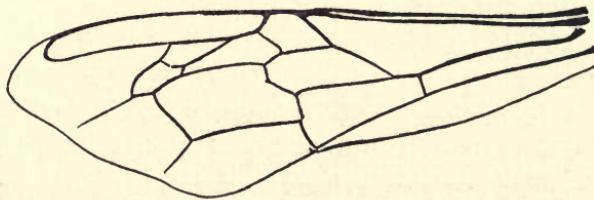


FIG. 5. Fore wing of honey bee (drone) showing complete cell at 3+.

cell interpolated (fig. 4); 2 show a complete new cell interpolated (fig. 5).

Of the 300 right fore wings 12 are torn; of the remaining 288: 120 show no variation (fig. 1); 71 show var. 2, var. 3, or

var 4, either in "very slight," "slight," "fair," "good" or "marked" degree or two or three of these variations in combination (figs. 2 and 3); 72 show var. 1 complete (fig. 3); 22 show var. 1 incomplete (fig. 2); 1 shows an almost complete new cell interpolated (fig. 4); 2 show a complete new cell interpolated (fig. 5).

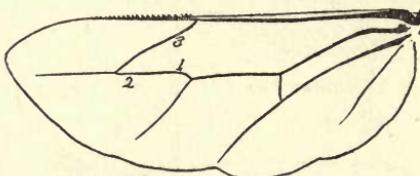


FIG. 6. Hind wing of honey bee (drone) showing normal venation and points of variation indicated by numbers.

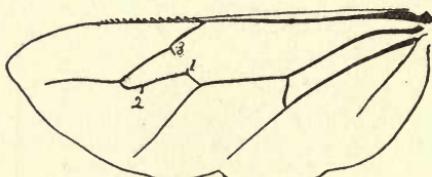


FIG. 7. Hind wing of honey bee (drone) showing vars. 1, 2, and 3.

The normal venation of the hind wings is shown in figures 1 and 6. The variations noted consist of the addition of a spur at points 1, 2, 3, or 4 (4 is at the left of 2, see fig. 8, C) "very slight," "slight," "fair," "good" or "marked" in degree of length, and of the interpolation of a new complete cell in the region occupied by the varying spurs.

Of the 300 left hind wings 12 are torn; of the remaining 288: 163 show no or only "very slight" variation (fig. 6); 82 show at least one (sometimes more) of var. 1, var. 2, var. 3, or var. 4 in condition called "slight" (fig. 7); 41 show at least one (sometimes more) of var. 1, var. 2, var. 3, or var. 4, in condition called "fair" or "good" or "marked" (fig. 7); 2 show the interpolation of a new complete cell (fig. 8).

Of the 300 right hind wings; 157 show no or only "very slight" variation (fig. 6); 87 show at least one (sometimes more) of vars. 1, 2, 3, or 4, in condition called slight (fig. 7); 45 show at least one (sometimes more) of vars. 1, 2, 3, or 4, in

degree called "fair," "good" or "marked" (fig. 7); 1 shows a complete new interpolated cell (fig. 8).

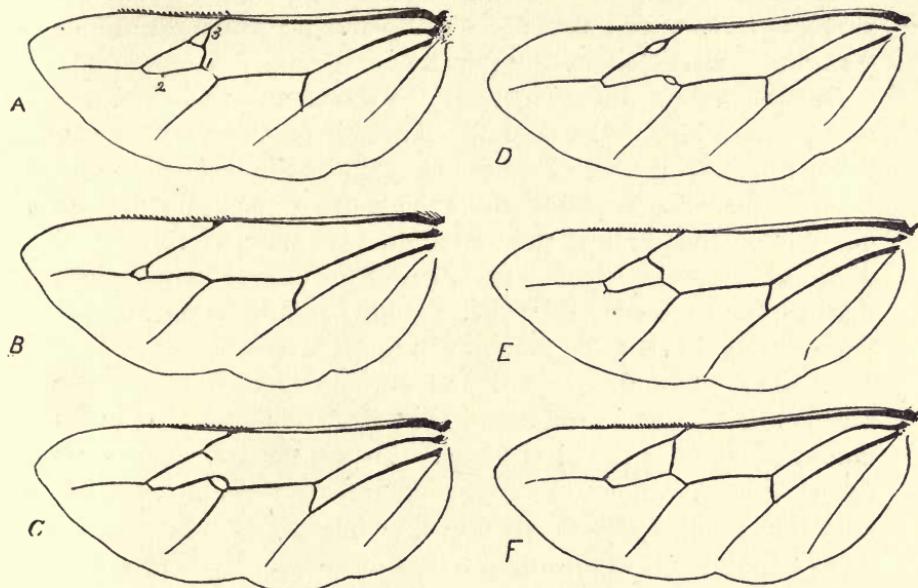


FIG. 8. Hind wings of honey bee (drone) showing interpolation of complete cells; *A*, complete cell at 3; *B*, complete cell at 2; *C*, complete cell at 1; *D*, complete cells at 1 and 3; *E* and *F*, complete cell formed by meeting of spurs 1, 3.

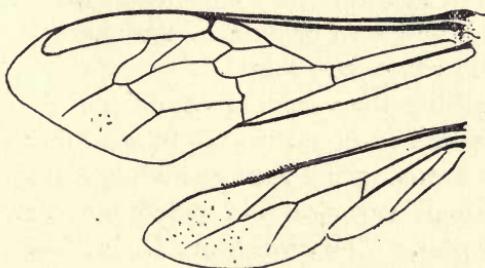


FIG. 9. Fore and hind wings of honey bee (worker) showing normal venation.

A lot of 300 workers from the same hive from which the above lot of drones was taken was examined for variation in the character of the venation of the wings. Of the 300 left fore wings: 288 show no variation (fig. 9); 2 show var. 1 incomplete;

1 shows var. 1 complete; 8 show var. 3 "very slight" or "slight"; 1 shows a complete new cell interpolated.

Of the 300 right fore wings: 293 show no variation (fig. 9); 1 shows var. 1 complete; 5 show var. 3 "very slight" or "slight"; 1 shows var. 3 "fair."

Of the 300 left hind wings, but one shows any variation, that being a case of "var. 2 slight." There is manifest a tendency toward the appearance of spurs indicated by the frequent angulation of the veins at points where the spurs occur in the drones, but that is the limit of the variation. Of the 300 right hind wings also but one shows a variation of the degree called slight that being also a case of "var. 2 slight." The same angulation of the veins is to be noted as in the left wings.

Another lot of drones (48) and workers (300) from another hive (Italians) was examined for the same conditions of variation in venation of the hind wings. Among the 300 workers no describable variation was found, simply the slight although manifest tendency to have the spur-bearing (in the drones) veins angulated thus affording traces of spurs. Among the 48 drones, on the contrary, the various spurs recorded for the previous lot from laboratory hives were present in various degrees of length, and five cases of the interpolation of complete new cells were noted (see fig. 8).

Another lot of 100 workers from still another hive (Germans) was examined, and no variation in the character of the venation of the hind wings was found.

Thus comparing the variation conditions of the wing venation in drones and workers, it is to be said that practically no variation exists among the workers, while a frequent and in a few cases extreme variation (interpolation of new cells) occurs among the drones. The drones are *males*, and are *parthenogenetically produced*; the workers are *females* (of arrested sexual development) and have *bi-sexual parentage*.

To ascertain what difference, if any, existed in the amount of variation (in venation of wings) between bees exposed to the struggle for existence and bees not yet so exposed, a lot of 200 drones from a hive (Italians) in a garden on the Stanford University campus taken from the capped brood cells at a time

when they (the drones) were just at point of issuance (some half issued from the cells, some gnawing at the caps, some just ready to begin breaking out) was examined.

Of the 200 left fore wings: 94 show no variation; 42 show spur 2, 3 or 4 in "very slight," "slight," "fair," "good," or "marked" degree, or two or three of these in combination; 32 show var. 1 complete; 1 shows var. 1 incomplete; 1 shows an almost complete new cell; 2 show a complete new cell; 16 show a break (interruption) in some vein (usually the vein carrying spur 4); 11 show a marked deformation of the venation (the veins in the discal area broken into small pieces and all askew) to such an extent as to be really a mutilation of the wing (fig. 10).

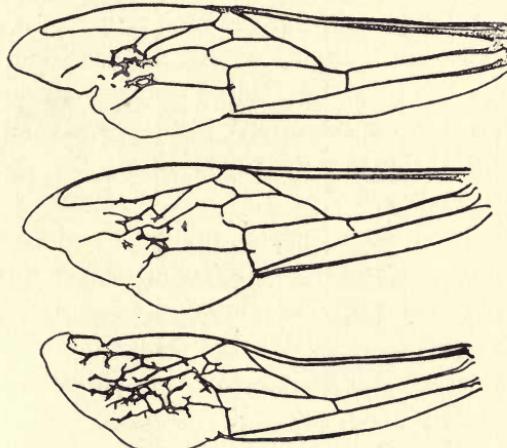


FIG. 10. Fore wings of honey bee (drones) showing extraordinary deformation of venation.

Of the 200 right fore wings: 95 show no variation; 56 show spur 2, 3 or 4 in "very slight," "slight," "fair," "good" or "marked" degree or two or three of these in combination; 23 show var. 1 complete; 1 shows an almost complete new cell; 15 show a break (interruption) in some vein; 12 show a marked deformation of the venation (the veins of the discal area being broken into small pieces and all askew) (fig. 10).

Of the 200 left hind wings: 139 show no or only "very slight" variation; 28 show at least one (sometimes more) of vars. 1, 2, 3 or 4 in condition called "slight"; 28 show at least

one (sometimes more) of vars. 1, 2, 3 or 4 in condition called "fair," "good," or "marked"; 1 shows an almost complete new cell; 6 show a complete new cell; 1 shows a break (interruption) in a vein.

Of the 200 right hind wings: 134 show no or only "very slight" variation; 30 show at least one (sometimes more) of vars. 1, 2, 3 or 4 in condition called "slight"; 28 show at least one (sometimes more) of vars. 1, 2, 3 or 4 in condition called "fair," "good" or "marked"; 1 shows an almost complete new cell; 6 show a complete new cell; 1 shows a deformation (only in less degree) like that shown in certain of the fore wings.

Also a lot of 54 workers just ready to leave their cells, were taken from the brood comb of a laboratory hive and examined for variation in the venation of the wings. There was found in no wing, fore or hind, right or left, a variation of the degree called "slight" (as used in discussing the previous lots), although a manifest tendency toward the appearance of a spur at point 2, reaching sometimes the condition of trace or "very slight" was apparent.

Another lot of 25 workers from the cells and 50 workers just issued from cells and acting as nurses (not yet having left the hive at all) taken from a hive (Italians) near Stanford University was examined for variation in the venation of the wings. In neither fore nor hind wings was any variation of the extent called "slight."

Thus it is apparent that it is not the action of a life and death selection which accounts for the differences in the amount of variation in drones and workers. As the workers in their constant going and coming outside the hive, carrying heavy loads of pollen and exposed to any dangers which slow or imperfect flight might induce, as capture by birds and robber-flies, may be fairly said to run much more risk in their life than the drones which make but a single brief flight each day (and that not every day), it might be thought or assumed that this strenuous life of the workers would tend to weed out by life and death selection every slight disadvantageous variation in the supporting skeleton (the venation) of the wings, all important organs in this outside life. But our workers from cells (not yet exposed to selec-

tion on basis of adult structures) show no more variation in wing venation than those which have been so exposed. It is also to be noted that our drones from cells show no more variation than the free flying ones except in one particular. That is in the presence among them, in the proportion of 11 to 200, of certain individuals whose front wings have a wholly abnormal venation, of the condition of a sort of mutilation or monstrosity of such a character as to prevent the full unfolding of the wing and probably its use at all as a flight organ. As the fore wings are the chief factors in the flight of bees, the hind wings being attached to them by hooks, in large degree moved by them and obviously auxiliary and subordinate to them, this variation probably produces a crippled individual quickly eradicated by nature or perhaps purposely by the keen-eyed and thrifty workers. At any rate we have never found such a crippled-winged drone in any lot of individuals taken in the "drone catcher" (which is a device fastened over the external opening of the hive and which snares any drone that voluntarily attempts to issue from the hive). For the rest of the variation the free-flying drones show practically no less, and of course no more, modification in venation than the ones taken from cells.

Practically, thus, the same amount of variation exists in the venation of the wings among free-flying drones and workers as exists among individuals which have just acquired their imaginal structure, which seems to mean nothing less than that this variation as manifest, as considerable and in a few cases as extreme as it is, and as common (*i. e.*, occurring in numerous individuals) as it is, is not sufficient to be of life and death value in the struggle for existence. In the exposure of the bees to the rigor of the factors which determine natural selection this variation in the skeletal framework of the wings, organs obviously unusually important in the relation of the bees to the outside world, does not afford a handle for the selective action of these factors.

It is of interest to note in passing the large importance attached by entomologists to the venation characters in the systematic study of insects, especially those in which the venation, as in the Diptera, Lepidoptera, and Hymenoptera (to which

order the bee belongs) has been specialized by reduction, *i. e.* where the veins have been reduced in number and degree of branching and inter-connection by cross-veins, so that the remaining vein framework is presumably in all of its details essential to the best performance of the wing's function, namely flight. This reliance on venation is not based on such theoretical grounds however, but on the practical one of experience and wide observation. In many of these specialized insects the venation is fairly uniform throughout a whole family, while practically never are describable differences in venation expected to be found within generic limits. In Comstock's Manual of Insects (the standard American systematic manual) the keys to the families of Diptera and Lepidoptera are nearly solely, and of Hymenoptera, largely based on venation. Thus variation in venation is to be looked on as important.

Measurements of Parts of Wing-veins.—Wishing to be able to give an accurate quantitative expression to some features of the variation of the wing venation, we have measured certain parts of veins whose limits are accurately established by subtending cross-veins, or by the forking or branching of the veins themselves. In order to determine the relation of any variation in these measurements to the varying size of the whole wing this size, as indicated by the measured length and breadth (or when impossible to get the length owing to battered and broken wing tips by the width alone), has been ascertained for all of

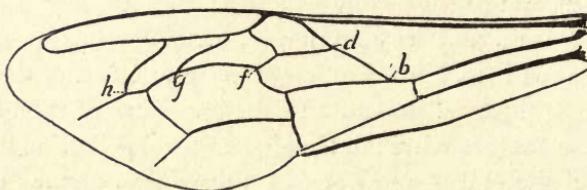


FIG. 11. Fore wing of honey bee (drone) with letters indicating subtending points on various veins.

the wings studied. While at first thought the dimensions of parts of the veins might be assumed to be directly related to, *i. e.*, a simple function of, the size of the wings, yet an inspection of the parts selected for measurement will suggest the pos-

sibility and even probability (a condition actually confirmed by the statistical study) of a variation in these dimensions due to the varying situation in the wing area of the cross veins or the varying earlier or later (in point of distance from the base of the wing) forking or branching of the veins, which should be wholly or nearly independent of the size of the wing.

In figure 11 are indicated the parts of veins measured, and the symbols by which these parts will be referred to in the tabulation of results. All measurements were made under magnification by one person using the same microscope, lenses and ocular micrometer throughout the work.

The breadth and the parts of veins indicated in figure 11 as *b-d*, *f-g*, and *g-h*, were measured in the right fore wings of 300 drones from the laboratory hive (Italians), (the same lot whose wings were mounted and studied for variation in character of venation with the results given on p. 214).

The frequency polygon showing graphically the variations in breadth (indicative of size of the whole wing) and the size or frequency of the various classes in this series of 294 individuals (six individuals had broken right fore wings) is as follows:

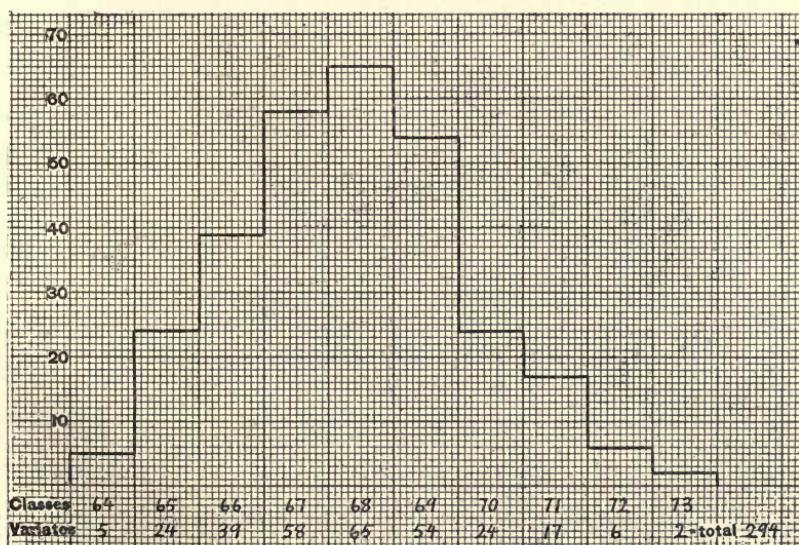


FIG. 12. Frequency polygon of the variation in width of the right fore wings of 294 drone honey bees taken from laboratory hive at one time; mean width 67.9 micrometer units; index of variability 1.8; coefficient of variation 2.65.

The mean breadth is 67.9 (units of the micrometer), the mode (most frequent breadth) is 68, the standard deviation 1.8 (units or the micrometer) and the coëfficient of variation 2.65. The frequency curve is a nearly symmetrical unimodal curve, *i. e.* variation in size of the wing follows the law of error.

The frequency polygon showing the variations in length of the vein part, *b-d* (see fig. 11) and the frequency of the various classes in a series of 300 individuals is as follows:

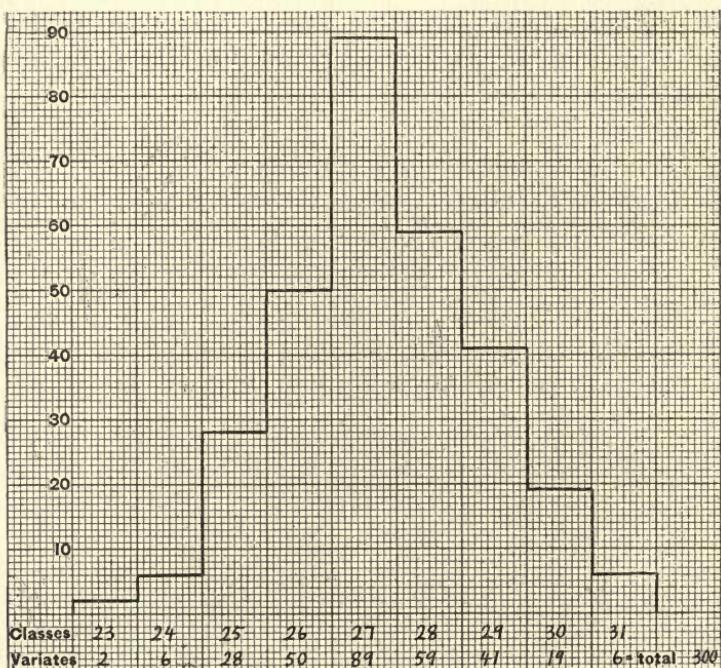


FIG. 13. Frequency polygon of the variation in measurement *b-d* (see Fig. 11) in the right fore wings of 300 drone honey bees taken from laboratory hive at one time; mean length of this vein part 27.5 micrometer units; index of variability 1.422; coefficient of variation 5.24.

The mean length of this definitely subtended bit of vein is 27.5 (units of micrometer scale) the mode (most frequent length) 27 (units of the micrometer), the standard deviation 1.42 + (units of micrometer) and the coefficient of variation 5.24. There is thus a relatively much larger variation in this measurement than in the breadth of the same wings.

The frequency polygon showing graphically the variation in the vein part $f-g$ (see fig. 11) is as follows (fig. 14):

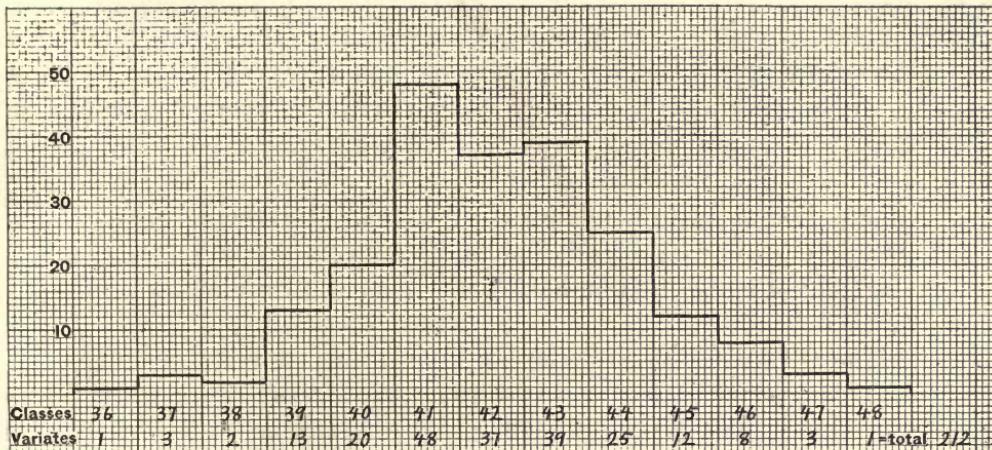


FIG. 14. Frequency polygon of the variation in measurement $f-g$ (see fig. 11) in the right fore wings of 212 drone honey bees taken from laboratory hive at one time; mean length of this vein part 42.1 micrometer units; index of variability 2.027; coefficient of variation 4.81.

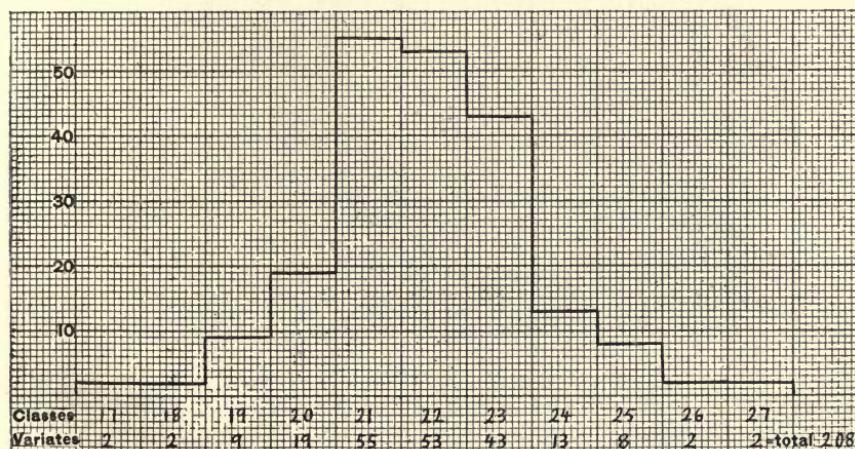


FIG. 15. Frequency polygon of the variation in measurement $g-h$ (see fig. 11) in the right fore wings of 208 drone honey-bees taken from laboratory hive at one time; mean length of this vein part 21.9 micrometer units; index of variability 1.61; coefficient of variation 7.3.

The mean length is 42.1, the mode 41, the standard deviation 2.027, and the coefficient of variation 4.81. This variation is about as extensive as that of measurement $b-d$, and nearly twice as large as that of the wing's breadth.

The frequency polygon showing graphically the variation in the vein part $g-h$ (see fig. 11) may be seen in fig. 15.

The mean length is 21.9, the mode 21 (with 22 almost as frequent and 23 only one-fifth less frequent), the standard deviation 1.61, and the coefficient of variation 7.3. Thus the variation in the length of this definitely subtended bit of vein is three times as great as the variation in breadth (a direct factor of size) of the wing and one-half larger than the variation in certain other vein parts.

The same dimensions of the right fore wings namely, breadth, and parts of veins, $b-d$, $f-g$ and $g-h$, were measured in a lot of 300 workers taken from the laboratory hive (Italians), the same lot in which the variations in the character of the venation of the wings was studied with the results given on p. 217. In addition the lengths of 98 of these wings could be measured (no

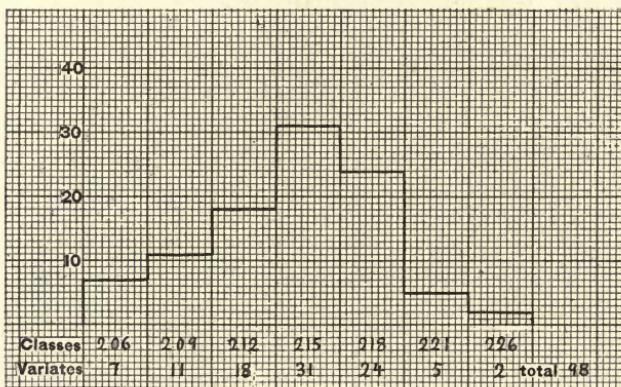


FIG. 16. Frequency polygon of the variation in length of the right fore wings of 98 worker honey-bees taken from laboratory hive; mean length 214.3; index of variability 2.37; coefficient of variation 1.1. *

lengths could be got in the case of the drones because of the breaking of the wing tips in the drone catcher) and thus a more certain criterion of the extent of variation in size (indicated for the drones by the breadth) obtained.

The frequency polygon showing graphically the variation in length of 98 (202 individuals had the wing tips battered) right fore wings in this lot of workers, and the frequency of the various classes may be seen in fig. 16.

The mean length is 214.3 (units of the micrometer), the mode (most frequent length) 215 (units of the micrometer), the standard deviation 2.37 (units of the micrometer) and the coefficient of variation 1.1. The frequency curve follows fairly well for such a short series the theoretical one of the law of error.

The frequency polygon showing the variation in the breadth of 296 wings is as follows :

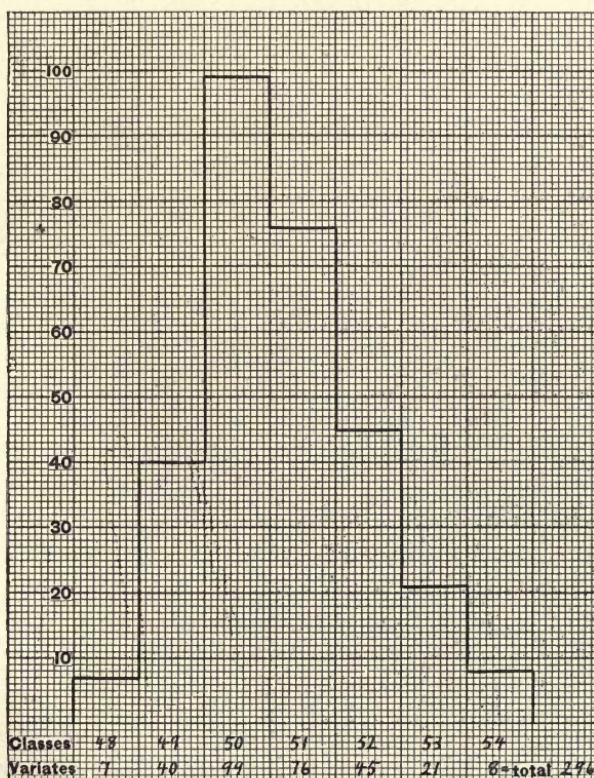


FIG. 17.

The mean breadth is 50.7, the mode 50, the standard deviation 1.3, and the coefficient of variation 2.57. Thus comparing

the variation in breadth and length it is to be noted that the variation in breadth is twice as large as that in length, which indicates that we do not err on the side of obtaining too low a coefficient of variation in size of the wing when we accept the C. V. for the breadth as a criterion of the C. V. for size, an assumption forced on us in the case of the drones because of the torn wing tips making the length determinations impossible.

The frequency polygon showing the variation in length of the vein part $b-d$, is as follows:

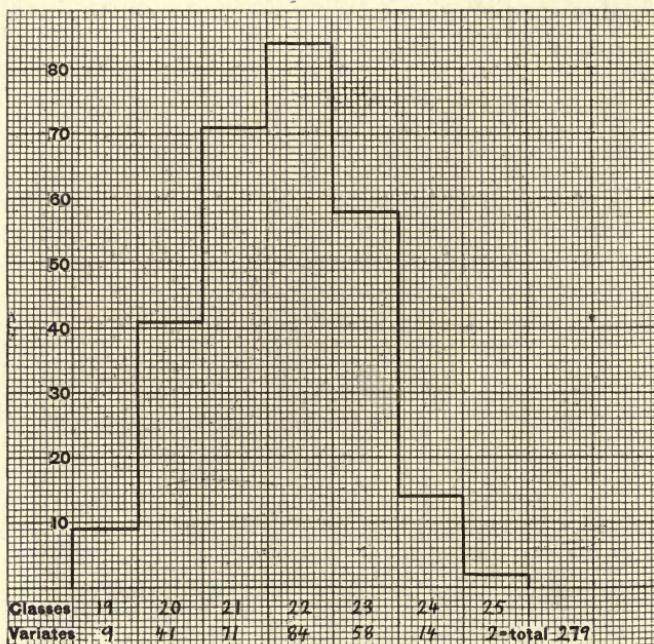


FIG. 18. Frequency polygon of the variation in measurement $b-d$ (see fig. 11) in right fore wings of 279 honey bee workers taken from laboratory hive at one time; mean length of this wing part, 21.7 micrometer units; index of variability, 1.223; coefficient of variation, 5.63.

The mean length is 21.7, the mode 22, the standard deviation 1.22, and the coefficient of variation 5.63. Here, as in the drones, the variation of the part of a vein definitely subtended by the forking of the vein or origin of a branch, is more than twice as large as the variation in size of the wing as indicated by the variation in breadth.

The frequency polygon showing the variation in length of the vein part *f-g*, is as follows :

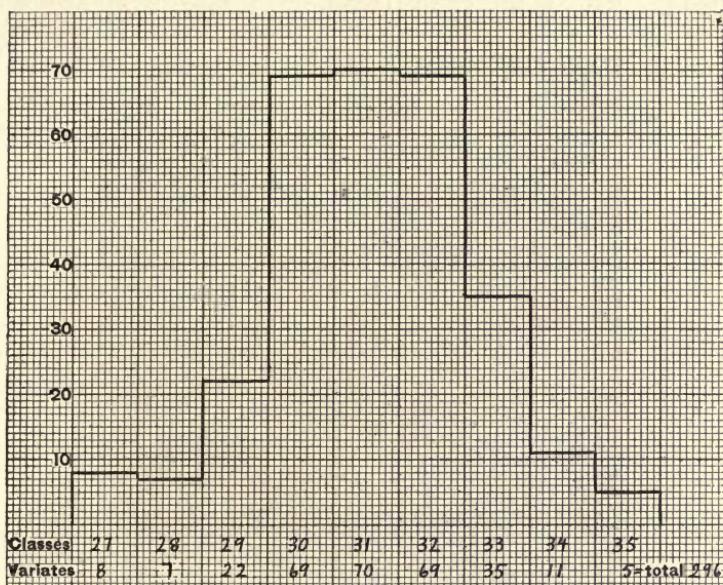


FIG. 19. Frequency polygon of the variation in measurement *f-g* (see fig. 11) of right fore wings of 296 honey bee workers taken from laboratory hive at one time; mean length of this wing part, 31.8 micrometer units; index of variability, 1.732; coefficient of variation, 5.446.

The mean length is 31.8, the mode 31, the standard deviation 1.73, and the coefficient of variation 5.44.

The frequency polygon showing the variation in the length of the vein part *g-h* may be seen in fig. 20.

The mean length is 18.1, the mode 18, the standard deviation .959, and the coefficient of variation 5.3.

Several other smaller lots of drones and workers from different hives were examined for this variation in length of vein parts and size of whole wing, the right fore wings being removed, mounted and measured under magnification. These lots agree so closely with the conditions just tabulated for the larger lot from the laboratory hive that it will be unnecessary to give space here to the specific data for these several smaller lots. In all these lots the variation in the parts of the veins are

approximately twice as large as the variation in the breadth (= size) of the wing, and the variation in drones and workers is (relatively) nearly the same, with the preponderance slightly

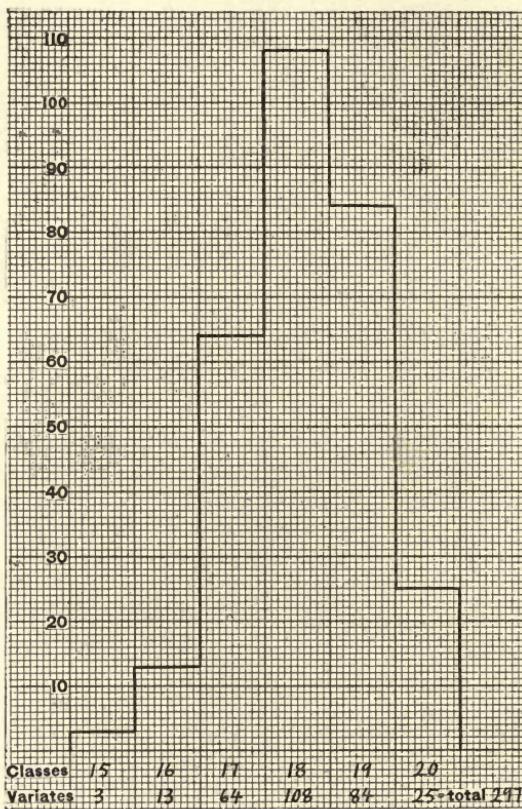


FIG. 20. Frequency polygon of the variation in measurement *g-h* (see fig. 11) of the right fore wings of 297 worker honey bees taken from laboratory hive at one time; mean width, 18.1 micrometer units; index of variability, .959; coefficient of variation, 5.3.

with the workers, a condition identical with that in the larger, laboratory-hive lot.

Variation in Number of Hooks on Costal Margin of Hind Wings.—The two wings of each side are fastened together, when outstretched in flight or in "ventilating," by a series of small strong recurved spines or hooks along the costal margin of the hind wing (figs. 1 and 21) which "catch" or "hook

over" the thickened anal (hinder margin) of the middle one-third of the fore wing. The fastening together of the wings during flight so as to insure perfect synchrony of movement and to effect practically a one-wing-on-a-side specialization is not unique with the bees, but occurs among other Hymenoptera, as the ants and wasps, also in the caddice flies and jugate moths,



FIG. 21. Part of costal margin of hind wing of honey bee much magnified, to show hooks.

where the joining of the wings is loose and little perfected, depending on the overlapping of the base of the hind wing by the backward projecting subtriangular flap or "jugum" of the base of the fore wings, and also among the frenate moths by the well known frenulum or "bridle." This tying together of the fore and hind wings is, in effect, a step toward that specialization shown by the Diptera, the possession of but a single wing on each side. In the swiftest and most effective flyers among the Lepidoptera, the hawk-moths (*Sphingidae*), the hind wings are greatly reduced, being indeed wholly subordinate to the fore wings, on which the flight function really depends. Among the Hymenoptera, too, this specialization has gone far so that in the ants and the bees the marked reduction in the size of the hind wings and their perfect attachment to the fore wings by means of the hooks and anal ridge contrivance result in subordinating them wholly to the fore wings. Without doubt the effective flight of the honey bees depends largely on this particular specialization of the flight organs, so that the costal hooks of the hind wings on which the perfect tying together of the wings depends, are to be looked on as important structures, small and simple as they are. Flight has everything to do with the successful life of the bees, and the costal hooks have much to do with successful flight. An optimum condition of number and character of costal hooks is certainly advantageous to the bee; variations from this optimum are to be looked on as disadvantageous. Natural selection ought to find in the variation

of these hooks "handles" for its work, if it ever is to take into account variations in small but distinct characters which are in immediate relation to the external environment of the organism.

We have determined the variation in the number of costal hooks in the hind wings of 300 drones from a laboratory hive (Italians), the same lot whose wings have been studied for variation in character of venation and in linear dimensions of vein-parts (see pp. 214 and 223).

The variation in 279 left hind wings (21 of the 300 individuals had torn wings) is graphically shown by the following frequency polygon:

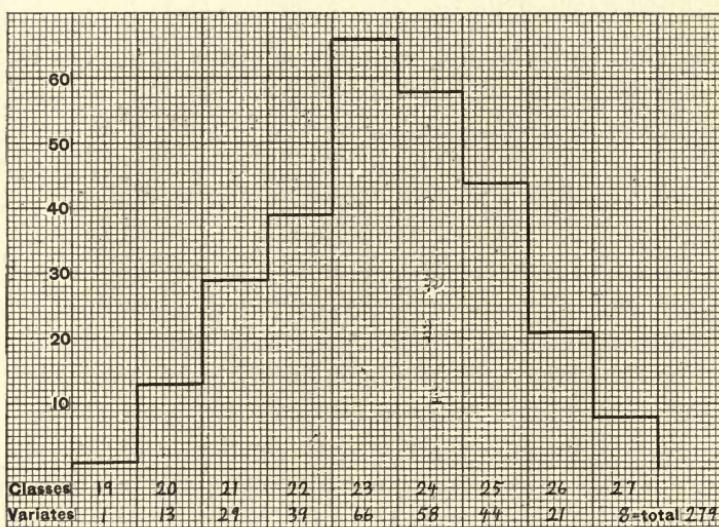


FIG. 22. Frequency polygon of the variation in number of costal hooks of left hind wings of 279 drone honey bees taken from laboratory hive at one time; mean 23.36; index of variability 1.695; coefficient of variation 7.25.

The range in number of hooks is from 19 to 27; the mean is 23.36, the mode 23, the standard deviation 1.695, and the coefficient of variation 7.25. Eighty-two individuals ($29\frac{2}{5}$ per cent.) have a smaller number of hooks than the mode (and than the mean) while one hundred and thirty-one (47 per cent.) have a larger number. The number having the mode is sixty-six ($23\frac{3}{5}$ per cent.).

The variation in 286 right hind wings (14 individuals had torn wings) is graphically shown in the following frequency polygon:

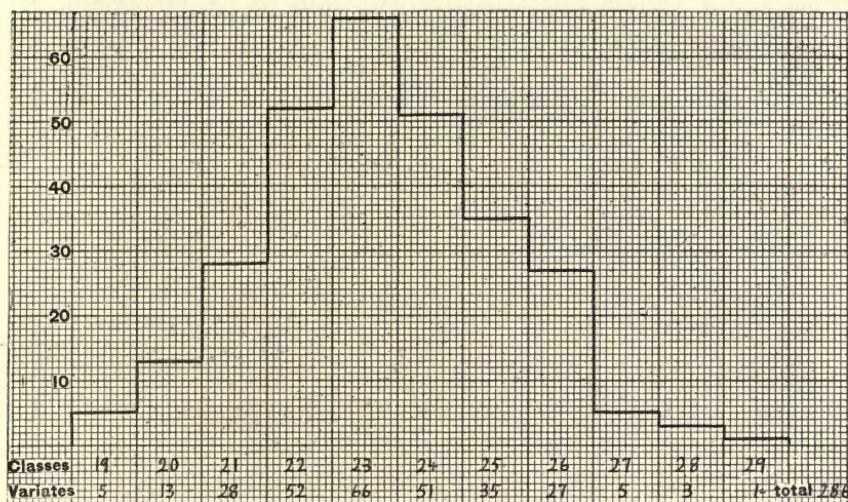


FIG. 23. Frequency polygon of the variation in number of costal hooks of the right hind wings of 286 drone honey bees taken from laboratory hive at one time; mean 23.26, index of variability 1.838; coefficient of variation 7.9.

The range is from 19 to 29, the mean 23.26, the mode 23, the standard deviation 1.838 and the coefficient of variation 7.9. Ninety-eight individuals ($34\frac{2}{5}$ per cent.) have a smaller number of hooks than the mode (and than the mean) while one hundred and twenty-two ($42\frac{3}{5}$ per cent.) have a larger number. The number having the mode is sixty-six (23 per cent.), the same number as in the left wings.

In 300 workers (Italians) from the same laboratory hive, the lot whose wings have been studied for variation in venation (see pp. 217 and 226), the variation in number of costal hooks in 299 left hind wings is graphically shown in the frequency polygon on the following page (fig. 24).

The range is from 17 to 26, the mean 21.13, the mode 21 (with 22 almost as frequent), the standard deviation 1.581, and the coefficient of variation, 7.48.

The variation in 293 right hind wings (7 individuals of the lot

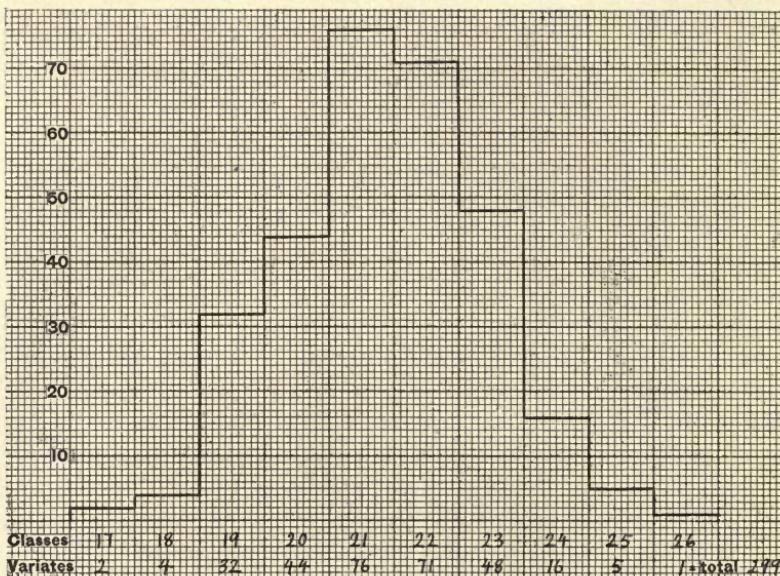


FIG. 24. Frequency polygon of the variation in number of costal hooks of the left hind wings of 299 worker honey bees taken from laboratory hive at one time; mean 21.13; index of variability 1.581; coefficient of variation 7.48.

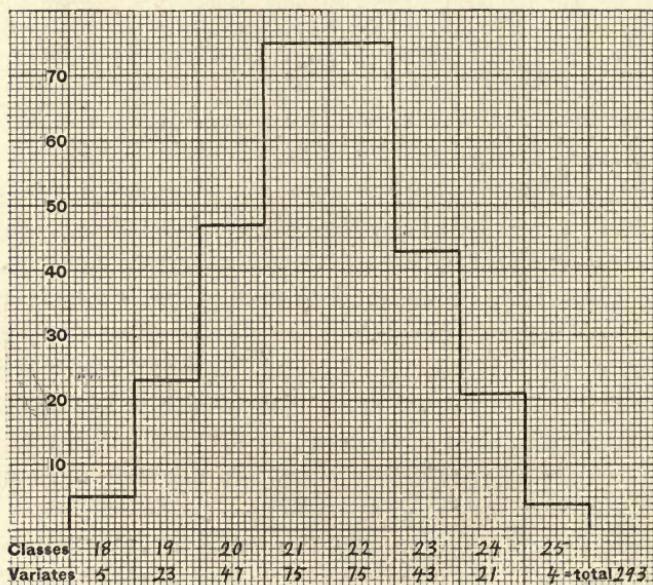


FIG. 25. Frequency polygon of the variation in number of costal hooks of the right hind wings of 293 worker honey bees taken from laboratory hive at one time; mean 21.4; index of variability 1.462; coefficient of variation 6.8.

had torn wings) is graphically shown in the frequency polygon on p. 234 (fig. 25).

The range is from 18 to 25, the mean 21.4, the mode 21 and 22 (these two numbers of the same frequency), the standard deviation 1.462 and the coefficient of variation 6.8.

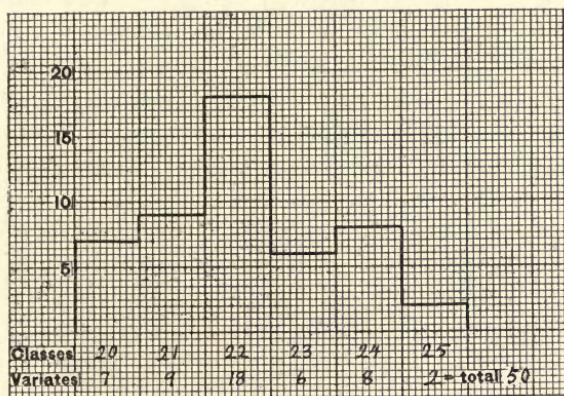


FIG. 26. Frequency polygon of variation in number of costal hooks of the left hind wings of 50 worker honey bees taken from hive No. 10 at one time; mean 22.1; index of variability 1.36; coefficient of variation 6.15.

From another hive on Stanford University campus were taken a lot of 50 workers and a lot of 50 drones. The varia-

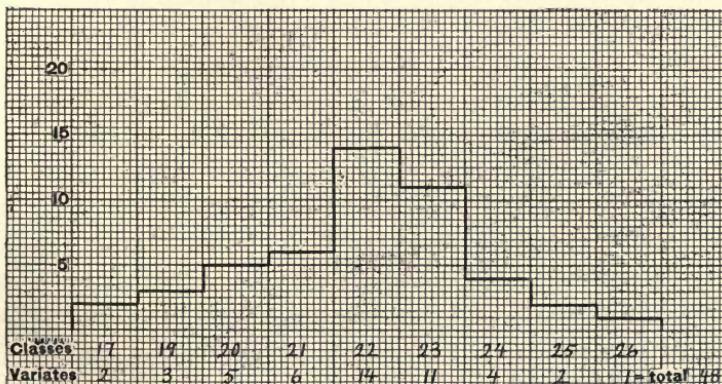


FIG. 27. Frequency polygon of the variation in number of costal hooks of the left hind wings of 48 drone honey bees taken from hive No. 10 at one time; mean 21.1; index of variability 2; coefficient of variation 9.53.

tion in costal hooks of the left hind wings in these lots is as follows:

Workers: Range 20 to 25, mean 22.1, mode 22, standard deviation 1.36, coefficient of variation 6.15 (see fig. 26).

Drones: Range 17 to 26, mean 21.1, mode 22, standard deviation 2, coefficient of variation 9.53 (see fig. 27).

Five lots of ten workers each, taken from five different hives and put together to form one mixed lot of 50 show the following variation in the hooks of the left hind wings; range 16 to 24, mean 20.6, mode 20, 21 and 22, standard deviation 1.85, coefficient of variation 9 (see fig. 28). It is interesting to note

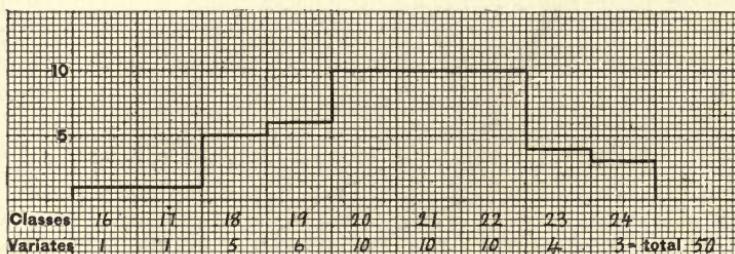


FIG. 28. Frequency polygon of the variation in number of costal hooks of the left hind wings of 50 worker honey bees taken in lots of 10 from five different hives; mean 20.6; index of variability 1.85; coefficient of variation 9.

how much larger the coefficient of variation is for this lot of individuals of miscellaneous heredity, five times as much heredity, if it may be so expressed, being represented in this lot of 50 workers as in the one of 50 workers taken from a single hive (mentioned in the paragraphs above); the coefficient of variation for the 50 workers representing five different mothers being 9, while for the 50 workers of one mother it is but 6.15. This illustrates well the need for homogeneous material whose history is known in the comparative study of any variation within the limits of a species, as the relative variability in the sexes, of one character as compared with another and the like. In our comparative study of the variation in workers and drones, the two largest lots, of 300 individuals each, were taken from the same hive at approximately the same time (about November 1) and all are offspring of one mother.

To compare the variation in hooks among individuals not yet issued from the hive, *i. e.*, not yet having made any use of the hooks in their life, but nevertheless with the definite complement of hooks fully developed for each individual, we examined a lot of 200 drones taken from cells in our laboratory hives (Italians) the same lot previously studied for variation in venation (see p. 218).

The frequency polygon graphically showing the variation in the hooks of the left hind wing in these individuals is as follows :

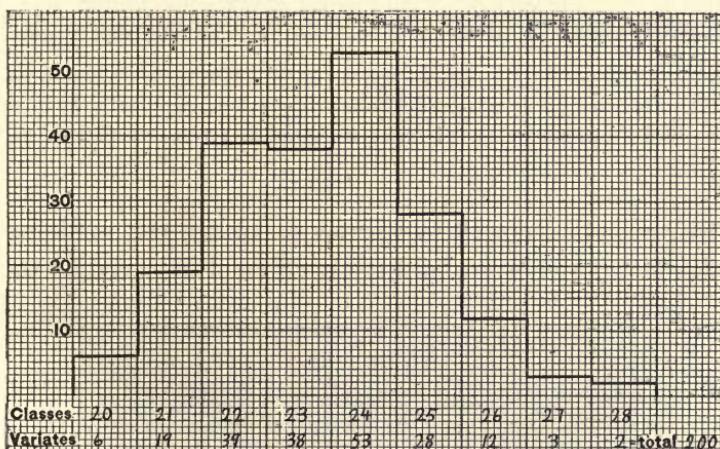


FIG. 29. Frequency polygon of the variation in number of costal hooks of the left hind wings of 200 drone honey bees taken from cells in laboratory hive at one time; mean, 23.36; index of variability 1.6; coefficient of variation 6.8.

The range in number of hooks is from 20 to 28, the mean 23.36, the mode 24, the standard deviation 1.6, and the coefficient of variation 6.8.

The variation in the right hind wings is graphically shown in the frequency polygon on p. 238 (fig. 30). The range is from 19 to 28, the mean 23.15, the mode 23 (with 24 practically equally frequent), the standard deviation 1.71, and the coefficient of variation 7.38.

The variation in a lot of 50 (approx.) workers taken from cells in our laboratory hive was determined. In the left hind wings it is as shown graphically in the frequency polygon on p. 238 (fig. 31).

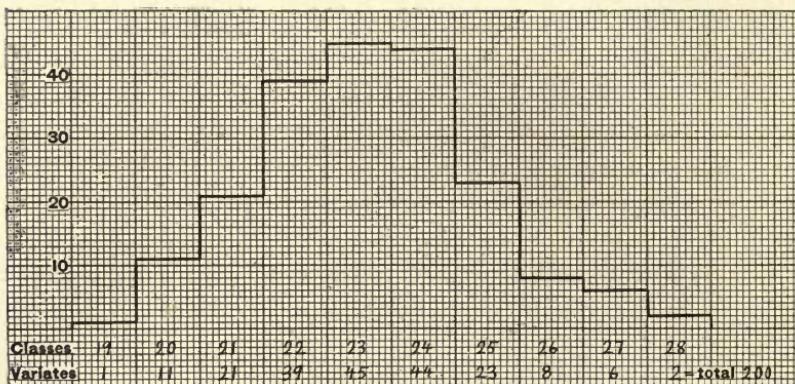


FIG. 30. Frequency polygon of the variation in number of costal hooks of the right hind wings of 200 drone honey bees taken from cells in laboratory hive at one time; mean 23.15; index of variability 1.71; coefficient of variation, 7.38.

The range is from 18 to 28, the mean 20, the mode 20, the standard deviation 1.19, and the coefficient of variation 6.

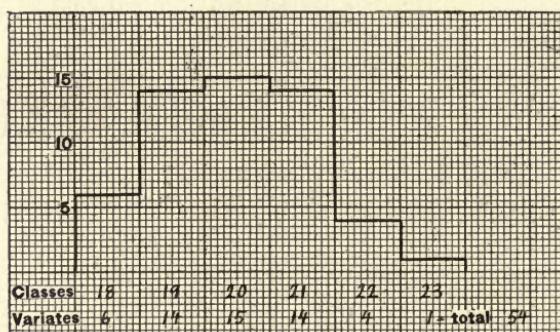


FIG. 31. Frequency polygon of the variation in number of costal hooks of the left hind wings of 54 worker honey bees taken from cells in laboratory hive; mean 20; index of variability 1.19; coefficient of variation 6.

In the right hind wings it is as shown by the frequency polygon on p. 239 (fig. 32). The range is from 16 to 22, the mean 19.6, the mode 20, the standard deviation 1.24, and the coefficient of variation 6.33.

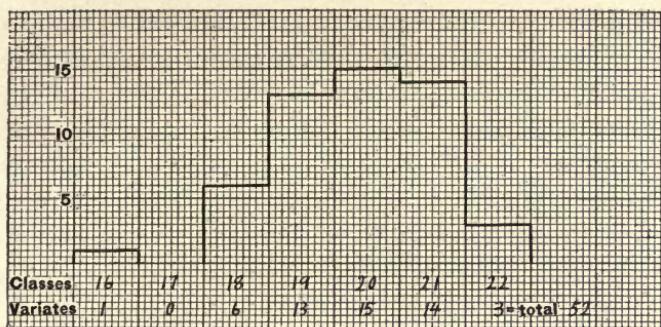


FIG. 32. Frequency polygon of the variation in number of costal hooks of right hind wings of 52 worker honey bees taken from cells in laboratory hive; mean 19.6; index of variability 1.24; coefficient of variation 6.33.

In another lot of 74 workers taken from cells in another hive the variation in hooks is as follows :

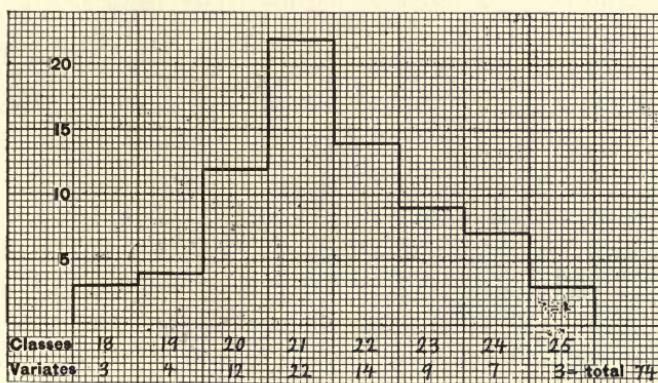


Fig. 33. Frequency polygon of the variation in number of costal hooks of the left hind wings of 74 worker honey bees taken from cells and among young in hive No. 8 at one time; mean 21.48; index of variability 1.637; coefficient of variation 7.62.

The range in left wings is from 18 to 25, the mean 21.48, the mode 21, the standard deviation 1.637, and the coefficient of variation 7.62.

Comparing now the variation in the number of costal hooks (whose importance in relation to the successful life of the bee is indicated on p. 231) on the hind wings of individuals which have been exposed to the struggle for existence, *i. e.*, have tested in

some measure the advantage or disadvantage of variations in the number of these hooks, with the variation in these hooks in the case of individuals which have not been exposed to the strenuous life outside the hive, *i. e.*, which have certainly not been selected on a basis of variation in these hooks, we find that in all measures of this variation, namely, in extreme range, in the mean, and the mode, the standard deviation (index of variability) and in the ratio (coefficient of variation) derived from the mean and the deviation, practical identity obtains in the case of both drones and workers. That is, the statistical study of the variation in this character shows *no evidence* of a selection by Nature among exposed individuals on a basis of variations in this character.

Comparing the variation in hooks in drones (males) and workers (females) we find practical correspondence in degree of this variation. In the range, mean and mode, to be sure, the workers show lesser figures but this is obviously simply due to the smaller size of the wings of the workers, and the standard deviation and coefficient of variation show that in relative degree or ratio, the variation is nearly equal in the sexes, the drones showing a slightly higher variability coefficient in both the exposed lots of individuals and the non-exposed lots.

This comparison also indicates the slight preponderance of variation in this character among the parthenogenetically produced individuals (which are the males) as contrasted with the individuals (workers) of bisexual parentage. Thus we have a definitely ascertained case, where, in the same species, individuals of bisexual parentage (results of amphimixis) show no greater, indeed show less variation than individuals parthenogenetically produced.

Correlations, Bilateral, Metemeric, and Otherwise, in the Variations of the Wings.—In examining the variation in character of venation, linear dimension of vein-parts and number of costal hooks on hind wings in the honey bee, to determine the correlation conditions in these variations, we have limited our work by not undertaking to determine mathematical expressions for these conditions as would be possible by the biometric methods of Pearson, *et al.*; we present merely certain direct statements of comparison.

Considering first variations in character of venation (for the nature of these variations see p. 214, et seq.).

Of the 7 cases of extreme variation consisting of the interpolation of a new complete or nearly complete cell in one or the other of the fore wings (4 in left, 3 in right) in a lot of 300 drones from laboratory hive, the opposite wing in 5 cases shows no variation while in 2 it shows only "slight" variation (slight spur at 2, 3 or 4). Of the right fore wings (in this lot) 84 show "var. 1 complete" (entire absence of a short cross vein) while 79 left fore wings show this variation. Of the individuals showing this condition in either right or left wing 47 show it also in the opposite wing, while 15 individuals show "var. 1 complete" in one wing coincidentally with "var. 1 incomplete" in the other, or "var. 1 incomplete" in both.

In the matter of the correlation of the variations in the hind wings in this lot of 300 drones, of the 3 extreme cases of the interpolation of a new complete cell in one wing (2 in left, 1 in right) in 2, the other wing shows no variation and in 1 it shows "var. 1 fair." In 105 right wings there is a spur at 1 "slight" to "marked," and such a condition occurs in 102 left wings. Of these cases the condition occurs coincidentally in both wings in 71 cases. So much for bilateral correlation of variations in character of venation in this lot.

Considering now the conditions of metamerie correlation in the same lot, we note that in the 7 (extreme) cases of interpolation of a new cell in the fore wing, the same individual shows in no case the extreme case of the interpolation of a cell in the hind wing of the same side (or of the other side for that matter), so that it is also true that of the 4 cases of an interpolation of a new cell in a hind wing none shows a similar extreme variation in either front wing.

In the lot of 200 drones taken from cells in another hive, of the 2 cases of extreme variation consisting of the interpolation of a new complete or nearly complete cell in one or the other of the fore wings (1 in left, 1 in right), the opposite wing in neither case shows any variation. In the several (12 in right fore wing, 11 in left fore wing), curious cases of still more extreme variation, reaching what may fairly be called a mutilation

(in extreme cases actually preventing the full unfolding and flattening of the wings, see fig. 10 and p. 219) both wings are affected in all but one instance. Can this be a mutilation or deformation acquired by the pupal wing in the cell due to some cramping condition, or perhaps to the manipulation of the still damp unexpanded wings by the nurses in the few moments immediately after the emergence of the bee from its cell? Of the right fore wings 23 show "var. 1 complete" (entire absence of a short cross vein) while 32 left fore wings show this condition. Of the individuals showing this condition in either right or left wing, sixteen show it also in the opposite wing, while one shows "var. 1 complete" in one wing coincidentally with "var. 1 incomplete" in the other; or "var. 1 incomplete" in both.

In the hind wings of this lot of drones from cells the following conditions occur: Of the 12 cases in which a complete cell is interpolated in one or the other wing the opposite wing has a similar cell in 3 cases, shows no variation in one case, and some variation in five cases. A deformation somewhat like that referred to as occurring (in several cases) in the front wing occurs in the right wing of one individual coupled with only "slight" variation in the opposite wing. In 12 right wings there is a spur at 1 "slight" to "marked," and such a condition occurs in 16 left wings. Of these cases the condition occurs coincidentally in both wings in 7 cases.

Considering now the metamerie conditions in the same lot we note that in the two cases of interpolation of a new cell in the fore wing, the same individual shows in neither case the similar interpolation of a cell in the hind wing of the same (or other) side, so that it is also the fact that in the 12 cases of such an interpolation of a cell in the hind wing, no individual shows a similar variation in the fore wing of the same (or other) side (one case shows an incomplete cell in one fore wing). In one case of the 12 cases however both fore wings show the "deformation" condition. Also in the two deformation cases in a hind wing both individuals show "deformation" of both fore wings.

Taking up the correlation conditions of the variation in number of costal hooks in the hind wings, we find in the lot of 300 drones from the laboratory hive, in which the modal numbers

are 23 and 24 (see p. 232) that 175 individuals have both right and left wing with either 23 or 24 hooks, while 123 have either the right or left wing with less than 22 or more than 25. Of these the cases where both wings have under 22 are 14, and both over 25 are 13, thus making a total of 27 cases out of 123 where the second member of a pair is *also* as marked in variation as the first.

In the lot of 200 drones taken from cells in another hive, the modal numbers being 23 and 24, 48 individuals have both right and left wings with either 23 or 24 hooks, while 74 have either the right or left wing with less than 22 or more than 25. Of these the cases where both wings have under 22 are 10, and where both have over 25 are 5 thus making a total of 15 cases out of 74 where the second member of a pair is *also* as marked in variation as the first.

In the lot of 300 workers from the laboratory hive, it is plain from the frequencies of the various classes (see p. 233) that 20, 21, 22 and 23 are the more usual numbers of hooks. In 201 individuals neither wing has fewer than 20 nor more than 23 hooks, in 98 individuals either the right or left wing has under 20 or more than 25. Of these both wings have under 20 hooks in 10 cases and both over 23 in 5 cases thus making a total of 15 in which the second member of the pair is *also* as marked in variation as the other member. In only one case has one wing under 20 and the other over 23; there is one case of 20-26, one of 18-23, and two of 19-23 in the lot.

It is certainly surprising to find such relatively small bilateral and metemeric correlation in these insect variations when one recalls the immense amount of bilateral and metemeric correlation (often in great detail) which characterizes the class of insects to-day, a correlation which we presume to have come about through the known evolutionary factors.

Summary.—To sum up in few words the conditions noted to exist in the honey bees, we find: (a) that in certain important structural characters, viz., the venation (skeletal frame work) of both fore and hind wings and the costal hooks which hold, in flight, the hind wings to the fore wings, there is a marked degree of variation which we can confidently term

strictly blastogenic variation; (*b*) that the variation in character of venation, consisting of the addition of various spurs or parts of veins (persistent remnants of phyletically lost veins (?)) and, more rarely, of interpolated new complete or nearly complete cells, is *marked* in the drones, which are *males* that are *parthenogenetically produced*, and is almost *nil* in the workers, which are *females* (with ovaries in arrested development) that are the offspring of *bi-sexual parentage*; (*c*) that the variation in lengths of certain parts of veins, subtended by cross veins or by the forking of the veins themselves, is more than twice as large as the variation in size of the wing (as indicated by the length and breadth, or breadth alone) and is nearly the same in both drones and workers; (*d*) that the variation in number of costal hooks of the hind wings is considerable and is about the same in both drones and workers; and (*e*) that the variation in character of venation, length of vein-parts and number of costal hooks in individuals fully developed, but taken from cells at the time of their natural issuance, and thus not yet exposed in free flying condition to the rigors of the struggle for existence (*i. e.*, the action of natural selection), is no greater than, but is practically the same as in individuals which have been exposed for a longer or shorter time to dangers of natural enemies, and of the necessities of long and sustained flight (in a word which have tested the worth of the wing structure as it subserves the important function of flight), thus indicating that these variations in wing characters do not have a life and death selective value. The only variations in wing character in which the individuals taken from cells (unexposed to the struggle for existence) exceed free-flying individuals (exposed to the rigor of selection among individuals) are those curious deformations, to be looked on as malformations acquired during development (due to cell pressure or accident) or if as blastogenic variations then of the nature of sports or discontinuous variations of extreme type. No free-flying form showed such a deformation of venation and it is probable that no bee with such malformed venation can successfully fly.

Variations in the Number of Hooks and Character of Venation in the Wings of Male Black Ants.—The ants are insects with com-

plete metamorphosis, the adults (imagines) issuing from protected pupæ, with all parts in definitive and unchangeable condition (after the brief expanding and drying of wings, legs, etc., immediately on appearance). Variations in the adult are to be looked on as congenital.

A lot of 200 male winged ants of one species (undetermined), collected at one time from one place, has been studied for variation in the number of hooks on the costal margin of the hind wings, for variation in the dimensions of the fore wings and restricted parts of the veins, and for variation in the character of the venation in the hind wings. These ants had issued for their mating and distributing flight and had fallen exhausted on the surface of the water in a watering trough. They were probably members of a single community, or, at most, of two or three neighboring nests.

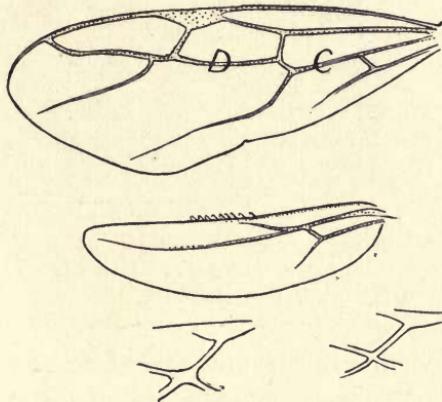


FIG. 34. Fore and hind wings of male black ant, showing normal venation, lettered parts of veins referred to in data of measurements, hooks on costal margin of hind wing, and three degrees of fusion of certain veins referred to in text.

The hind wings of ants are provided with a series of small, strong curved spines or hooks along the costal margins of the wings (fig. 34). When the wings are expanded these hooks grasp a thickened vein in the hinder margin of the fore wings and securely tie or hold the two wings of each side together, thus making them vibrate perfectly synchronously, or indeed as a single wing. The hooks are undoubtedly important structures

in the flight apparatus. These hooks vary in number in the individuals of this lot, the following frequency polygons showing the range and character of this variation¹ for both right and left hind wings. (See figs. 35 and 36.)

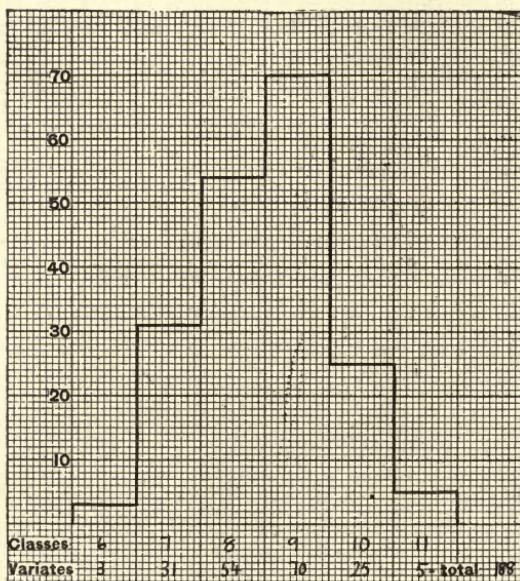


FIG. 35. Frequency polygon of the variation in number of costal hooks of left hind wings of 188 male black ants (sp. undetermined); mean 8.5; index of variability 1.048; coefficient of variation 1.23.

The range in each wing is thus from 6 to 11 hooks, a single 5-hook right wing occurring, while the mode in one wing, the right, is 8 and in the other 9. It will be noted that in the right wing, 9, in the left wing, 8, are nearly equally represented with the mode, so that the true condition existing in this species is probably bi-modal with the two modes, 8 and 9, being successive instead of separated numbers. The frequency curve is, considering the brevity of the series, a fairly symmetrical one, and in a large series would probably nearly coincide with the theoretical curve (determined by the law of error) indicating

¹ Where hooks were broken off or jerked out of their insertion pits they were counted as present; they were present at the time of the appearance of the adult, *i. e.*, congenitally present.

that this character of number of hooks is in a stable condition, tending neither manifestly to increase or decrease.

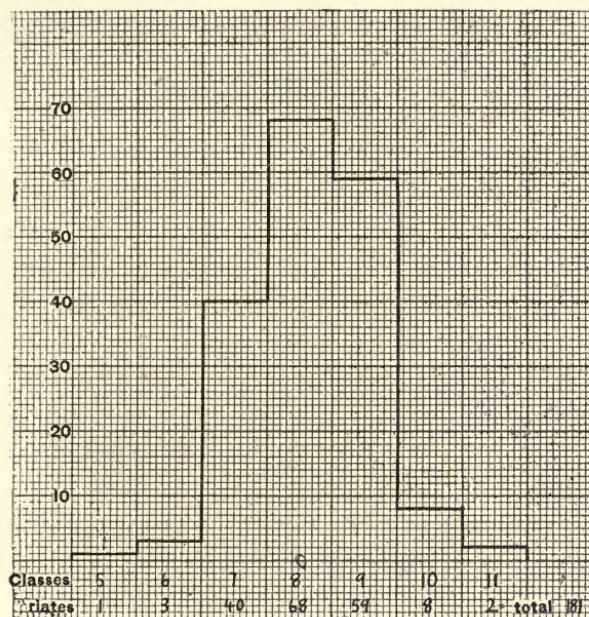


FIG. 36. Frequency polygon of the variation in number of costal hooks of the right hind wings of 181 male black ants; mean 8.7; index of variability 1.086; coefficient of variation 1.25.

Referring to the correlation between right and left wing in this character of number of costal hooks 90 individuals (out of 189) have each wing with 8 or 9 (the double mode) while 99 have at least one wing departing from the mode. Of these 99 individuals with one or both wings varying, 21 have both wings with less than 8 hooks, 9 have both wings with more than 9 hooks, while 3 have one wing with less than 8 and the other wing with more than 9 hooks. Thus there is an obvious right and left correlation, *i. e.*, bilateral symmetry, in the variations.

In going over the hind wings to count hooks, it was apparent to the eye that there existed a variation in the degree of coalescence of the radial and medial veins at a certain point of touching (see fig. 34). The wings can be readily and fairly divided into three classes based on differences in degree of this coales-

cence, this varying degree being indicated as much coalescence, median coalescence, very little coalescence. Correlating this character in right and left wings it is found that in 144 individuals both wings exhibited the same degree of coalescence of the veins, in 54 individuals one wing was median with the other either much or very little, and in no individual did one wing show much and the other very little. Of the 144 cases of identical coalescence in both wings 74 were median, 43 much and 23 very little on both sides; of the 54 cases of a combination of median with one of the extremes, the combination was median + much in 30 individuals and median + very little in 24 individuals. The right and left correlation, *i. e.*, bilateral symmetry, of the variations in this character of a modification in venation, is thus seen to be a nearly perfect one.

The variations in the measurements of the fore wings are indicated by the frequency polygons which follow. Four measurements were made (with micrometer, the wing being mounted flat and examined under the microscope) for each wing, viz., length, width, the length of a part of the cubital vein subtended by a cross vein and a point of forking (indicated as *C*)



FIG. 37. Frequency polygon of the variation in length of left fore wings of 191 male black ants collected at one time in one place; mean 89 micrometer units; index of variability 3.28; coefficient of variation 3.7.

in fig. 34), and the length of the sharply subtended part of another vein indicated as *D* in fig. 34. The differences in the measurements of length and breadth indicate variations in actual

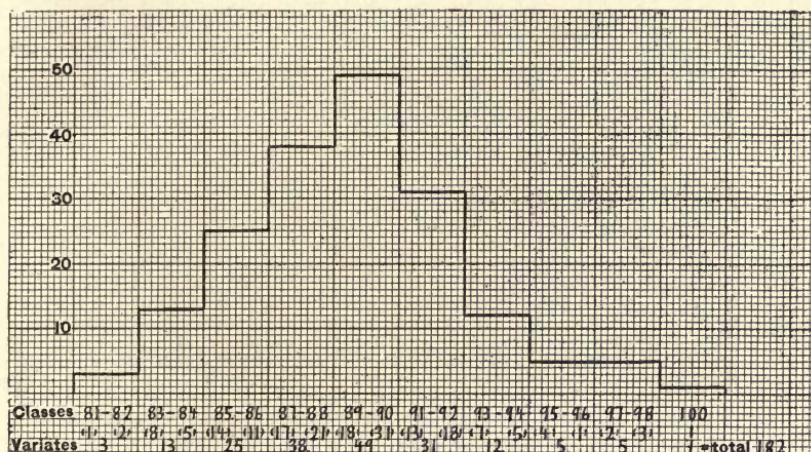


FIG. 38. Frequency polygon of the variation in length of the right fore wings of 182 male black ants collected at one time in one place; mean 90 micrometer units; index of variability 3.61; coefficient of variation 4.

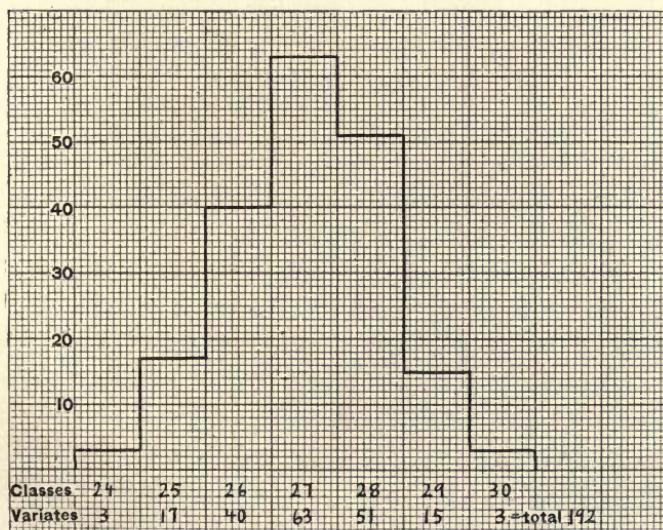


FIG. 39. Frequency polygon of the variation in width of left fore wings of 192 male black ants collected at one time in one place; mean 27.03 micrometer units; index of variability 1.19; coefficient of variation 4.4.

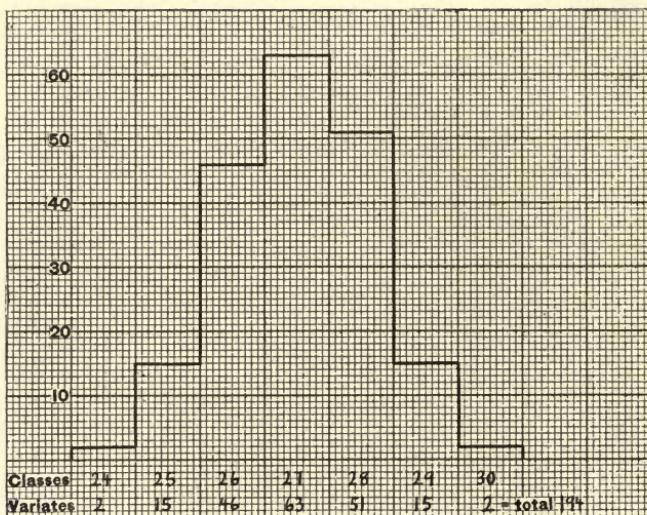


FIG. 40. Frequency polygon of the variation in width of the right fore wings of 194 male black ants, collected at one time in one place; mean 27.02 micrometer units; index of variability 1.14; coefficient of variation 4.22.

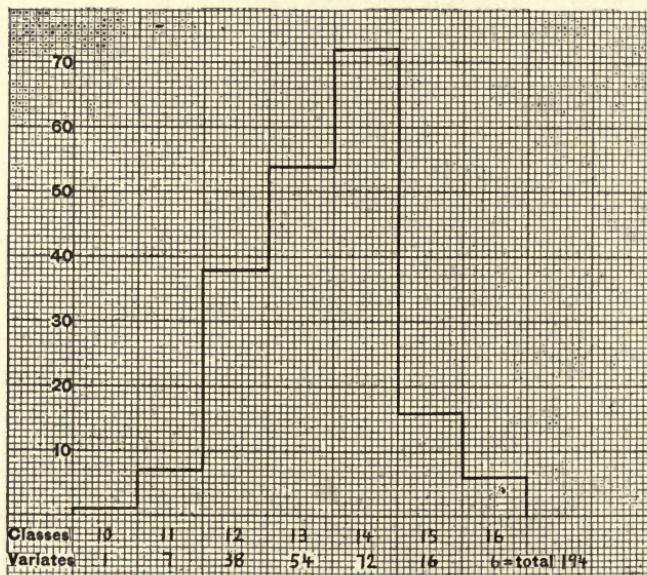


FIG. 41. Frequency polygon of the variation in measurement *C* (see fig. 34) in left fore wings of 194 male black ants, collected at one time and in one place; mean 13.34 micrometer units; index of variability, 1.119; coefficient of variation 8.4.

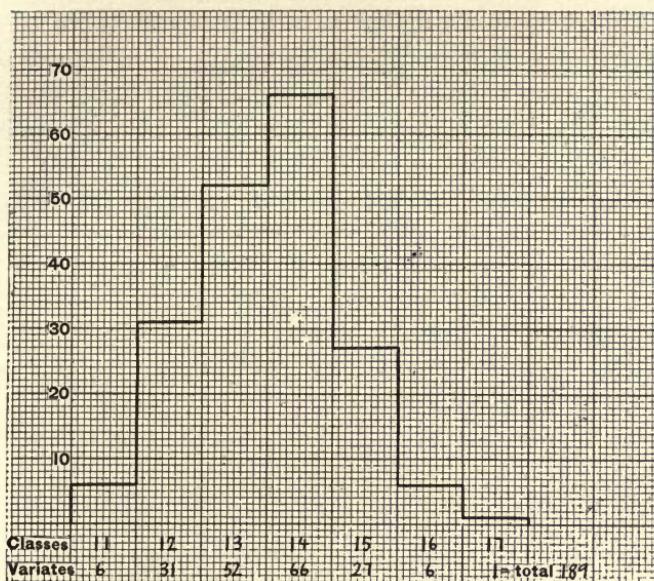


FIG. 42. Frequency polygon of the variation in measurement *C* (see fig. 34) in right fore wings of 189 male black ants, collected at one time in one place; mean 13.53 micrometer units; index of variability 1.144; coefficient of variation 8.5.

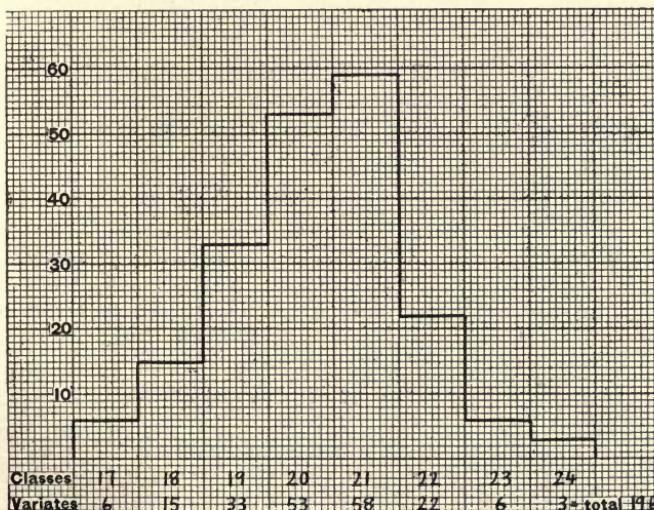


FIG. 43. Frequency polygon of the variation in measurement *D* (see fig. 34) of the left fore wings of 196 male black ants, collected at one time in one place; mean 20.3 micrometer units; index of variability 1.396; coefficient of variation 6.87.

size of the wings while differences in measurements *C* and *D* enable us to see if the variation in length of certain vein parts (as between cross veins, points of branching, etc.), are directly proportional to the wing size or have an independent variation of their own. The polygons showing the range and mode of the variation for each of these form dimensions are as follows: Polygon of length left wing, fig. 37; polygon of length right wing, fig. 38; polygon of width left wing, fig. 39; polygon of width right wing, fig. 40; polygon of meas. *C* left wing, fig. 41; polygon of meas. *C* right wing, fig. 42; polygon of meas. *D* left wing, fig. 43; polygon of meas. *D* right wing, fig. 44.

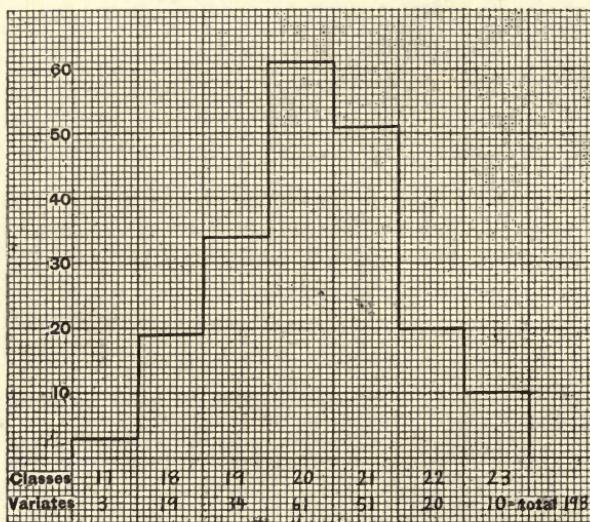


FIG. 44. Frequency polygon of the variation in measurement *D* (see fig. 34) of right fore wings of 198 male black ants, collected at one time in one place; mean 20.2 micrometer units; index of variability 1.33; coefficient of variation 6.58.

Determining for the sake of fair comparison the coefficients of variation for each of the form dimensions measured we find them to be the following: Length, for left wing 3, right wing 4; width, left wing 4.4, right wing 4.22; meas. *C*, left wing 8.4, right wing 8.5; meas. *D* left wing 6.87, right wing 6.58. Thus it is obvious that the variation in the vein parts, *i. e.*, the character or arrangement of the venation, is markedly larger

than the variation in actual size of the wing. If one of these kinds of variation may be looked on as in part acquired, *i. e.*, dependent directly on the nutrition or generally favorable or unfavorable circumstances during development of the individuals, it is the variation in size; the variation in character of the wing venation can certainly not be looked on as directly responsive to any external influence tending to modify in any particular way the course of the veins, structures which do not undertake the performance of their function at any time during immature life. But it is interesting to note that precisely this strictly blastogenic variation is markedly greater than that variation (in size) which might be considered to be in some part at least imposed on the individual during development.

The bilateral correlation in these dimensional wing variations seems, so far as indicated by the coefficients for right and left wings, to be close.

Variation in the Venation of Mosquitoes (*Grabhamia curriei* and *Culex incidunt*).—A lot of live pupæ of the western salt-marsh mosquito, *Grabhamia curriei*, were collected from a small, shallow brackish water puddle (3 feet by 5 feet by 4 inches deep) near an inlet on the salt marshes of San Francisco Bay, near Stanford University. These pupæ were brought into the laboratory in some of the water from the puddle, and the adults, which emerged in two and three days, were killed immediately. The wings of 50 males and 50 females were removed, mounted on glass slides, and their size and venation studied for variation. All measurements were made under magnification with an ocular micrometer. Mosquitoes are insects with complete metamorphosis, and the wings of the adults (imagines) appear in their full size and of definitive venational character immediately on their appearance (after expansion and drying).

The range of length of wings of the males was from 3.7 mm. to 4.3 mm., the mode 4.03 mm., the mean 4 mm., the standard deviation 1.15 mm. and the coefficient of variability 2.85 +. In the females the range is 3.4 mm. to 4.02 mm., the mode 3.8 + mm., the mean, 3.8 mm., the standard deviation 1.05 mm. and the coefficient of variability 2.76 +. Thus in size of the wing, the males (averaging a little larger actually) show a

slightly larger standard deviation and hence coefficient of variability than the females.

Although mosquitoes are insects with complete metamorphosis, in which the adult (imaginal) external structures are distinct from the larval, and appear at once, on the issuance of the adult from the pupal cuticle, in definitive condition, size of wings, as well as size of other parts of the body, is a character which may probably be influenced by the successful or faulty food getting of the metabolism of the larva, and thus be really in some degree an acquired variation instead of a strictly congenital one. In this particular instance the conditions of larval life were apparently as nearly as possible identical for all the larvæ of these studied adults; all the larvæ lived at the same time period in the same small pool. This identity of environment and life-conditions must have caused, to the extent that environment can cause, the same variations to be acquired by all the individuals, so that the lot should really show no difference (among its members) due to environmental influence. Any variation inside the lot ought, therefore, to be blastogenic in character. These blastogenic variations simply unfold and develop during the development of the individuals, remaining as unaltered in their relation to each other as they were in the egg, but, of course, now magnified to visibility by the very process of development. It should be noted in this connection that while nature or the experimenter may offer to a given lot of developing individuals identical amounts of food, under identical conditions of light, temperature, etc., there may be some individuals incapable of assimilating what is the optimum or minimum amount for others so that in so far as quantity of food constitutes environment and makes for development, these delicate individuals will not get their share. The experimenter can only work into the insect what the insect will accept, and only that part which the insect adopts may correctly be called his environment. We have bred silkworms which always had left-over scraps after each meal, while their neighbors left never a scrap; also larvæ which seemed *destined* to fail at moulting or pupating or issuing. Faulty metabolism and faulty food getting may occur under the *best* of environment, *but*, such

faulty performances are due to *congenitally* inadequate equipment, and if an individual takes unto itself as much of the environment as it can adopt, its differences from another individual which may have adopted more of the environment, are still congenital and comparable since the environment has differed only in so far as the congenital differences among individuals have forced it to differ. (For an example of this kind of blastogenic difference, see our account of the differences in weight, etc., of silk worms bred under identical conditions, *Science*, vol. XVIII, N. S., pp. 741-784, Dec., 1903.)

Taking now a character from the venation of the wings, we measured accurately the length of the third longitudinal vein from its origin at the anterior cross vein to its termination in the outer margin of the wing (the coalesced fourth and fifth branches of radius from the point of their intersection with the radio-medial cross vein to their termination in the outer margin) (see in fig. 45, from *a* to *b*) and found the following conditions:

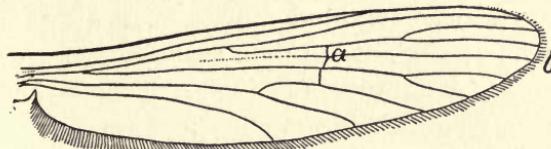


FIG. 45.

In the 50 males the range in length of this vein is .96 mm. to 1.32 mm., the mode 1.15, the mean 1.148, the standard deviation .59, and the coefficient of variability 5.15.

In the 50 females the range is .87 mm. to 1.17 mm., the mode 1.02, the mean 1.03, the standard deviation .62 and the coefficient of variability 6.03.

In this venational character the females show more variation than the males. To test the relation of the variation in length of this part of a vein with the variation in size of the wing it should be noted that while the coefficient of variability of the males for length (= size) of wing is only 2.85 the C. V. for the venational character is 5.15; while in the females the proportion is 2.76 to 6.03. Thus it is obvious that the venational character varies not only quite independently of the size char-

acter, which may be partly acquired, but varies about twice as much as this character.

To test this independence of variation in size and venational character in specific cases, the relation of the size to the mean and mode of size, and the relation of the measurement of the vein in relation to the mean and mode of this character may be noted for several individuals.

In the males the modal length of wing is 4.03 mm. and the mean 4 mm.; the modal length of the measured vein 1.15 mm. and the mean almost exactly the same, yet one male with wing 4.15 mm. long has the vein only 1 mm. long; another with wing 4.17 mm. long has the vein 1.13 mm. long; another with wing 4.21 long has the vein 1.16 long (wing lengths above mode and vein lengths below or at mode); two with wing 3.9 mm. long have vein 1.16 mm. long, another with wing 3.9 long has vein 1.31 long (wing lengths below mode and vein lengths above or at mode). In the females the modal length of wing is 3.8 mm. the mean the same, the modal length of vein 1.02 mm. the mean 1.03, yet several individuals have wing length of 3.9 mm. and a vein length of .98 mm. while one has a wing length of 3.85 mm. and a vein length of .87 mm. (wing lengths above mode and vein lengths below mode); and several have the wing 3.7 mm. long and the vein 1.05 mm. long while one with wing only 3.38 mm. long has the vein 1.14 mm. long (wing lengths below mode and vein lengths above mode). The variation in venation is manifestly not a simple function of the variation in size of wing in this lot of mosquitoes.

In a lot of adult mosquitoes, *Culex incidunt*, emerged in the laboratory from larvæ and pupæ collected at one time (September 16, 1901) from a watering trough, the variation in size (length) of wings and in length of third longitudinal vein (same as in case of the salt marsh mosquitoes referred to above) were studied in 30 males and 30 females.

In the males the length of third longitudinal vein ranges from .95 mm. to 1.2 mm. the mode being 1.03 mm. the mean 1.07, the standard deviation .63 mm. and the coefficient of variation 5.86.

In the females the length of the vein ranges from 1.02 to 1.27,

the mode being 1.2 mm., the mean 1.16 mm., the standard deviation .7 mm. and the coefficient of variation 6.03.

Thus in these short series the females show a slightly greater variability, in respect to this character, than the males. With the difference in variability so small, and with such short series, it is obvious that no generalization of worth can be made concerning the relative degree of variability in males and females. We are now attempting, however, to obtain lots of mosquitoes, each lot to be composed of individuals of one brood, and bred under identical environment so as to exclude, if possible, all but innate differences between the males and females. In these bred lots we shall examine quantitatively a number of varying characters of structures and pattern.

Variation of the Pattern of *Hippodamia convergens* (the Convergent Lady Bird).—The "lady-birds" are small, brightly and sharply marked beetles which often occur in large numbers, especially where their food, the soft-bodied plant-lice and young scale insects, abounds. In California these beneficial little beetles are abundant, the species *Hippodamia convergens* being one of the most familiar and numerous. This species, like some others, has the curious habit of assembling in winter time often in enormous numbers in a single mass or in several adjacent masses, in the axils of palm trees, in holes in stumps, or under leaves on the ground. About 40,000 individuals were collected on November 5, 1901, from such a hibernating assembly under leaves at the foot of an oak tree in the Sierra Morena Mountains, near Stanford University. All these individuals were inside of a circle twelve feet in diameter. Many more thousand specimens could have been taken from the same circle.

A series of individuals taken at random from this lot was examined and arranged on the basis of the variation in the character and number of the small but distinct black spots on the dorsal aspect of the red-brown elytra. The lady-birds have a complete metamorphosis, and the color pattern of the adults (imagines) appears in definitive and unchangeable form immediately (after the expanding and drying of the wings, legs and body-wall) on the issuance of the imago from the pupal cuticle. This color pattern is to be looked on as a strictly congenital

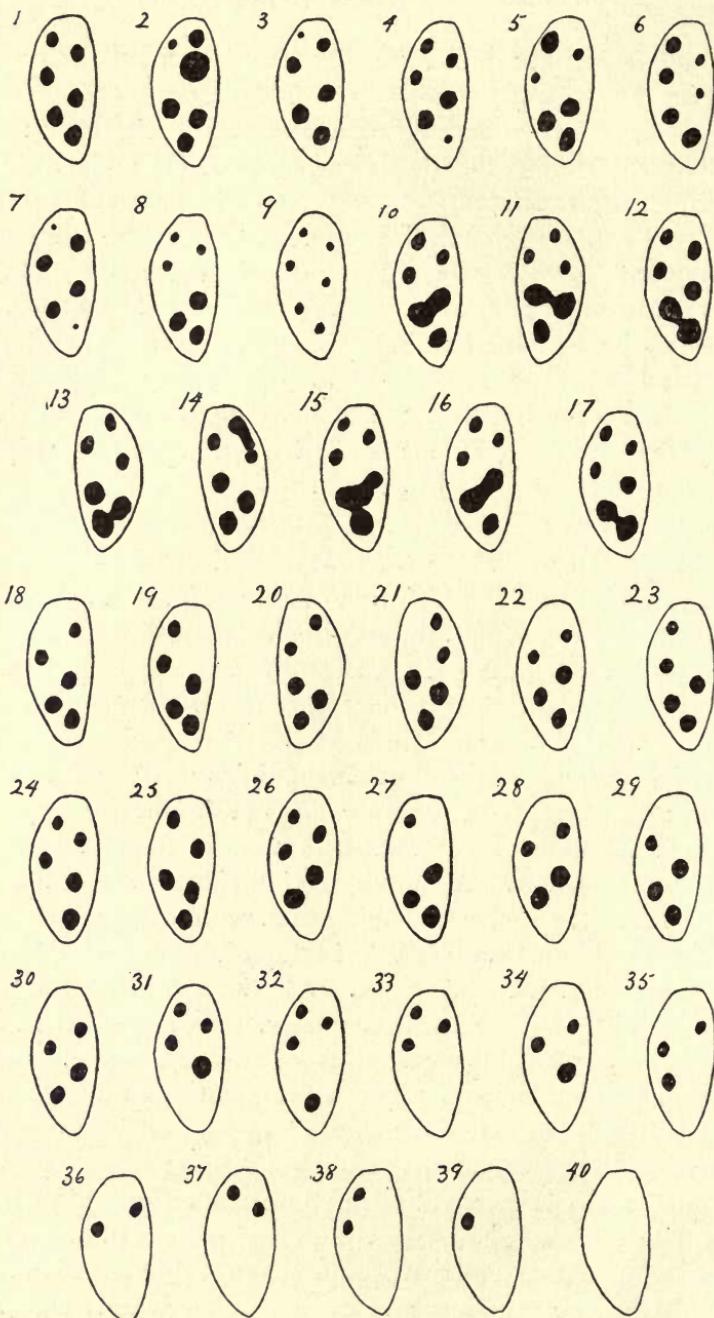


FIG. 46. Diagram showing var. in elytral pattern of the convergent ladybird, *Hippodamia convergens*; 1, the mode; 2-9, variations in size of spots; 10-17, variations by coalescence of spots; 18-40, variations by reductions in number of spots.

character, or certainly one not produced in response or reaction to any direct environmental chromatic influence, or to any selective influence, based on color pattern value, working during the immature life of the individuals.

A series of 1,031 individuals was classified on the basis of variation in the character and number of the elytral spots (see figs. 46 and 47) as follows:

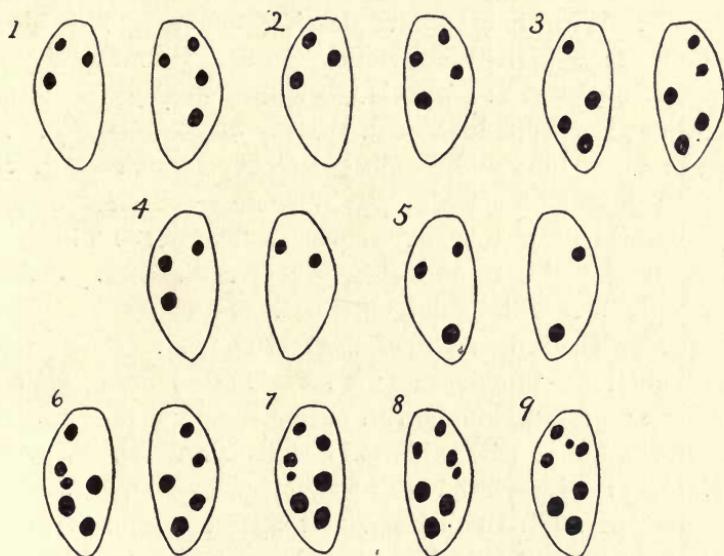


FIG. 47. Diagram showing var. in elytral pattern of the convergent ladybird, *Hippodamia convergens*; 1-5, vars. by reductions in number of spots differing in the two elytra; 6-9, variations by additions of spots.

Class A. With 12 spots (6 on each elytron) present and separate. (Total 900 individuals.) Subclass 1: 536 individuals with 12 spots present and separate, spots* 1^l and 1^r being slightly larger than spots 2^l, 2^r, 3^l, 3^r, spots 4^l, 4^r about twice the size of 2^l, 2^r and spots 5^l, 5^r, 6^l, 6^r, about equal in size to 4^l, and 4^r. Subclass 2: 211 individuals with spots 2^l, 2^r, 3^l, 3^r, reduced. Subclass 3: 106 individuals with spots 1^l, 1^r, 2^l, 2^r, 3^l, 3^r, re-

*The small super letters *l* and *r* refer to left and right elytra respectively, while the numbers 1, 2, 3, 4, 5 and 6 refer to the six spots on each elytron as present in the modal type (see fig. 46, 1), 1, 3, and 5 being the three spots in the outer longitudinal series numbered from the front (above in the figures) back, while 2, 4 and 6 are the spots of the inner longitudinal series.

duced. Subclass 4: 23 individuals with tendency to reduction of all spots. Subclass 5: 16 individuals with spots 2^l, 2^r, 4^l, 4^r, reduced. Subclass 6: 2 individuals with spots 6^l, 6^r, greatly reduced. Subclass 7: 1 individual with spots 1^l, 1^r, reduced. Subclass 8: 1 individual with spots 1^l, 1^r, 6^l, 6^r, barely showing. Subclass 9: 2 individuals with spot 3^r enlarged. Subclass 10: 1 individual with spot 3^l enlarged. Subclass 11: 1 individual with spot 4^r enlarged.

Class B. With some spots coalescing (total of 25 individuals). Subclass 12: 8 individuals with spots 4^l + 5^l and 4^r + 5^r coalescing. Subclass 13: 4 individuals with spots 4^l + 5^l coalescing. Subclass 14: 2 individuals with spots 4^r + 5^r coalescing. Subclass 15: 4 individuals with spots 5^l + 6^l, 5^r + 6^r coalescing. Subclass 16: 3 individuals with 5^l + 6^l coalescing. Subclass 17: 2 individuals with 5^r + 6^r coalescing. Subclass 18: 1 individual with spots 4^l + 5^l + 6^l and 4^r + 5^r + 6^r coalescing. Subclass 19: 1 individual with coalescence indicated between 1^r + 3^r.

Class C. Lacking some of the modal twelve spots (total of 70 individuals). Subclass 20: 2 individuals lacking *all* spots. Subclass 21: 8 individuals with only spots 3^l, 3^r present. Subclass 22: 2 individuals with only spots 1^l, 1^r, 2^l, 2^r, present. Subclass 23: 1 individual with only spots 1^l, 1^r, 3^l, 3^r, present. Subclass 24: 10 individuals with only 2^l, 2^r, 3^l, 3^r, present. Subclass 25: 6 individuals with only spots 1^l, 1^r, 2^l, 2^r, 3^l, 3^r, present. Subclass 26: 1 individual with only spots 2^l, 2^r, 3^l, 3^r, 4^l, 4^r, present. Subclass 27: 1 individual with only spots 1^l, 1^r, 2^l, 2^r, 3^l, 3^r, 4^r, present. Subclass 28: 1 individual with only spots 2^l, 2^r, 3^l, 3^r, 5^l, present. Subclass 29: 1 individual with only spots 2^l, 3^l, 3^r, 6^l, 6^r, present. Subclass 30: 1 individual with only spots 2^l, 2^r, 3^l, 3^r, 5^l, 5^r, present. Subclass 31: 1 individual with only spots 1^l, 1^r, 2^l, 2^r, 3^l, 3^r, 5^r, present. Subclass 32: 1 individual with spots 2^l, 2^r, 3^l, absent. Subclass 33: 1 individual with spots 2^l, 2^r, absent (extra spot between 3^l and 5^l). Subclass 34: 2 individuals with spot 1^l, absent. Subclass 35: 2 individuals with spots 1^l, 1^r, 6^l, 6^r, absent. Subclass 36: 1 individual with spots 6^l, 6^r, absent. Subclass 37: 2 individuals with spot 2^l, absent. Subclass 38: 9 individuals with spot 2^l, 2^r, absent. Subclass 39: 6 individuals with

spots 1^l , 1^r , absent. Subclass 40: 1 individual with spots 4^l , 4^r absent. Subclass 41: 1 individual with spot 3^r , absent. Subclass 42: 1 individual with spot 2^r , absent. Subclass 43: 1 individual with spots 3^l , 3^r , absent. Subclass 44: 2 individuals with spots 2^l , 2^r , 3^l , 3^r , absent. Subclass 45: 1 individual with spots 1^l , 1^r , 2^l , 2^r , absent. Subclass 46: 1 individual with spots 5^l , 5^r , 6^l , 6^r , absent. Subclass 47: 2 individuals with spots 1^l , 1^r , 1^l , 6^r , absent. Subclass 48: 1 individual with spots 5^l , 5^r , absent.

Class D. With more than the 12 modal spots (total of 38 individuals). Subclass 49: 18 individuals with one or more extra spots on right elytron; subclass 50: 13 individuals with one or more extra spots on left elytron; subclass 51: 7 individuals with one or more extra spots on both elytra.

Thus in a series of 1,031 individuals of this species (characterized in its description as possessing 12 elytral spots) 900 individuals possess 12 spots of which 536 agree in showing a certain common relative size of the spots which combination of number and relative size is the mode; the other 264 individuals possessing 12 spots have them in various different conditions of size. Of the remaining 131 individuals of the series, namely, those possessing more or less than 12 spots, or having some of these spots coalescing, the last condition, occurring in 8 different ways (combinations of coalescing spots) is present in 25 individuals; 70 individuals possess fewer than 12 spots, this condition occurring in 28 different ways, while 38 individuals possess more than 12 spots, of which 18 have the extra spots on the right elytron, 13 on the left elytron and 7 on both elytra. The total number of different ways in which more than 12 spots occur is not here given but is given later in the discussion of "aberrations of *Hippodamia convergens*" (p. 264).

In order to test the fairness of the estimate of frequencies (relative proportion) of the variations for a species, determined by the inspection of a limited series, we inspected and classified a second series of 751 individuals taken at random from the large collection's lot from which the 1,031 individuals just discussed were taken. Is a series of 1,000 fairly indicative of the

frequencies of the discoverable variations in a species? Are the proportions 70 to 1,031 and 38 to 1,031 really the proportions in which individuals with fewer than 12 and more than 12 spots, respectively, occur in the species *Hippodamia convergens* where the mode or normal is exactly 12 spots? The frequencies of the same classes of variations (given the same subclass numbers) discovered in the series of 1,031, in the second series of 751 are as follows:

Class A. With 12 spots (6 on each elytron) present and separate (total 673 individuals). Subclass 1: 289 individuals (mode); subclass 2: 186 individuals; subclass 3: 100 individuals; subclass 4: 6 individuals. New subclasses: 89 individuals showing various other combinations of reduced spots; 3 individuals showing a specially enlarged spot.

Class B. With some spots coalescing (total of 8 individuals). Subclass 12: 2 individuals; subclass 14: 1 individual; subclass 15: 4 individuals; subclass 16: 1 individual.

Class C. Lacking some of the modal 12 spots (total of 56 individuals). Subclass 20: 1 individual; subclass 21: 9 individuals; subclass 24: 10 individuals; new subclass: 2 individuals showing an extra spot while certain modal ones are lacking; new subclasses: 34 other individuals showing lacking of spots in 10 different combinations.

Class D. With more than the 12 modal spots (total of 22 individuals). Subclass 49: 5 individuals with one or more extra spots on right elytron; subclass 50: 10 individuals with one or more extra spots on left elytron; subclass 51: 7 individuals with one or more spots on both elytra.

As a further test of the capacity of a single series of a thousand (more or less) individuals collected "methodically at random," to represent fairly the character and frequencies of variations in some chosen structural characteristic of the organism, we have examined another lot of 1,730 individuals of the same species, collected October 25, 1902, near Stanford University (a year later than the lots of 1,031 and 751 already discussed). The individuals of this series were classified on the same basis as the other two series, and the classes and subclasses of corresponding character given letters and numbers corresponding

to those of the other series. The frequencies of the variations are as follows:

Class A. With 12 spots (6 on each elytron) present and separate (total 1,556 individuals). Subclass 1 (mode): 711 individuals; subclass 2: 493 individuals; subclass 3: 116 individuals; subclass 4: 55 individuals; new subclasses: various other combinations of reduction, and enlargement of spots, 181 individuals.

Class B. With some spots coalescing (total of 17 individuals). Subclass 12: 6 individuals; subclass 14: 1 individual; subclass 15: 4 individuals; subclass 16: 1 individual; new subclasses: 2 individuals showing other combinations.

Class C. Lacking some of the modal 12 spots (total of 116 individuals). Subclass 20: 16 individuals; subclass 21: 11 individuals; subclass 24: 24 individuals; subclass 26: 4 individuals; subclass 38: 24 individuals; subclass 39: 14 individuals; subclass 46: 5 individuals; new subclasses: 18 individuals in several other combinations each represented by one or two individuals.

Class D. With more than the 12 modal spots (total 36 individuals). Subclass 49: 8 individuals; subclass 50: 17 individuals; subclass 51: 11 individuals.

Comparing now this 1902 series of 1,730 individuals with the two series of 1901, the percentages of the various variation classes are as follows: Class A: 87+ per cent. in series of 1,031; 90— per cent. in series of 751; 90— per cent. in series of 1,730. Subclass 1 (the mode): 52 per cent. in series of 1,031; 38.5 per cent. in series of 751; 41 per cent. in series of 1,730. Class B: 2.5 per cent. in series of 1,031 individuals; 1.6 per cent. in series of 751 individuals; 1— per cent. in series of 1,730 individuals. Class C: 6.9 per cent. in series of 1,031 individuals; 7.5 per cent. in series of 751 individuals; 6.8 per cent. in series of 1,730 individuals. Class D: 3.7 per cent. in series of 1,031 individuals; 3 per cent. in series of 751 individuals; 2.5 per cent. in series of 1,730 individuals.

Thus there is obvious a close correspondence in frequencies of variation classes in the three series except in one conspicuous subclass, that of the mode. The mode class agrees well but

the modal subclass (modal in both) shows in the smaller series a frequency of 13.5 per cent. less than in the larger series.

“*Aberrations*.”—A considerable entomological literature cataloguing and describing “aberrations” has grown up, especially in connection with systematic lepidopterology. As an example of what may be done in this kind of refined systematic work the following 74 easily, briefly and definitely describable aberrations contained in a series of 1,782 individuals, being the combined two series of 1,031 and 751 just discussed, of *Hippodamia convergens*, all taken at one time in one locality (a circular area 12 feet in diameter), are presented. In this list Class D in each of the preceding series, composed of individuals possessing more than the 12 modal elytral spots is analyzed into its subclasses (which was not done in the previous discussion), but the subclasses of Class A (based on the differences in size of the exactly 12 spots present and distinct) are not taken into account. The aberrations (or variation classes) catalogued are based wholly on numbers of elytral spots and the varying combinations (varying by suppression or addition of particular spots) of spots which compose the number.

1. *Hippodamia convergens*. “Twelve-spotted lady-bird,” typical of the species description, each wing-cover being marked by 6 distinct and separate spots.

2. *H. convergens*; aberr. A₁. “Eleven-spotted lady-bird,” spot 3^l being absent.

3. *H. convergens*; aberr. A₂. “Eleven-spotted lady-bird,” spot 1^l being absent.

4. *H. convergens*; aberr. A₃. “Eleven-spotted lady-bird,” spot 2^l being absent.

5. *H. convergens*; aberr. A₄. “Eleven-spotted lady-bird,” spot 3^r being absent.

6. *H. convergens*; aberr. A₅. “Eleven-spotted lady-bird,” spot 2^r being absent.

7. *H. convergens*; aberr. A₆. “Eleven-spotted lady-bird,” spots 4^r and 5^r coalescing.

8. *H. convergens*; aberr. A₇. “Eleven-spotted lady-bird,” spots 5^l and 6^l coalescing.

9. *H. convergens*; aberr. A₈. “Eleven-spotted lady-bird,” spots 4^l and 5^l coalescing.

10. *H. convergens*; aberr. A₉. "Eleven-spotted lady-bird," spots 5^r and 6^r coalescing.
11. *H. convergens*; aberr. A₁₀. "Eleven-spotted lady-bird," spots 2^l and 2^r being absent, with an extra spot between 3^l and 5^l.
12. *H. convergens*; aberr. A₁₁. "Eleven-spotted lady-bird," an additional spot being present and uniting spots 5^r and 6^r.
13. *H. convergens*; aberr. B₁. "Ten-spotted lady-bird," spots 1^l and 1^r being absent.
14. *H. convergens*; aberr. B₂. "Ten-spotted lady-bird," spots 2^l and 2^r being absent.
15. *H. convergens*; aberr. B₃. "Ten-spotted lady-bird," spots 2^l and 3^l being absent.
16. *H. convergens*; aberr. B₄. "Ten-spotted lady-bird," spots 4^l and 4^r being absent.
17. *H. convergens*; aberr. B₅. "Ten-spotted lady-bird," spots 3^l and 3^r being absent.
18. *H. convergens*; aberr. B₆. "Ten-spotted lady-bird," spots 6^l and 6^r being absent.
19. *H. convergens*; aberr. B₇. "Ten-spotted lady-bird," spots 5^l and 5^r being absent.
20. *H. convergens*; aberr. B₈. "Ten-spotted lady-bird," spots 4^l and 5^l, 4^r and 5^r coalescing.
21. *H. convergens*; aberr. B₉. "Ten-spotted lady-bird," spots 5^l and 6^l, 5^r and 6^r coalescing.
22. *H. convergens*; aberr. C₁. "Nine-spotted lady-bird," spots 2^l, 3^l and 2^r being absent.
23. *H. convergens*; aberr. D₁. "Eight-spotted lady-bird," spots 1^l, 1^r, and 6^l, 6^r, being absent.
24. *H. convergens*; aberr. D₂. "Eight-spotted lady-bird," spots 5^l, 6^l, and 5^r, 6^r, being absent.
25. *H. convergens*; aberr. D₃. "Eight-spotted lady-bird," spots 2^l, 3^l, and 2^r, 3^r, being absent.
26. *H. convergens*; aberr. D₄. "Eight-spotted lady-bird," spots 1^l, 2^l and 1^r, 2^r being absent.
27. *H. convergens*; aberr. D₅. "Eight-spotted lady-bird," spots 4^l, 5^l, and 6^l, and 4^r, 5^r, 6^r coalescing.
28. *H. convergens*; aberr. D₆. "Eight-spotted lady-bird," spots 4^l, 5^l, and 4^r, 5^r being absent.

29. *H. convergens*; aberr. E₁. "Seven-spotted lady-bird," spots 4¹, 5¹, 6¹, 5^r, 6^r, being absent.
30. *H. convergens*; aberr. E₂. "Seven-spotted lady-bird," spots 4¹, 5¹, 6¹, 4^r, 6^r, being absent.
31. *H. convergens*; aberr. F₁. "Six-spotted lady-bird," spots 1¹, 5¹, 6¹, and 1^r, 5^r, 6^r, being absent.
32. *H. convergens*; aberr. F₂. "Six-spotted lady-bird," spots 1¹, 2¹, 3¹, and 1^r, 2^r, 3^r, being absent.
33. *H. convergens*; aberr. F₃. "Six-spotted lady-bird," spots 2¹, 4¹, 2^r, 4^r, 6^r, being present, and an additional spot between 2¹ and 3¹.
34. *H. convergens*; aberr. F₄. "Six-spotted lady-bird," spots 2¹, 3¹, 5¹, and 2^r, 3^r, 5^r, being present.
35. *H. convergens*; aberr. G₁. "Five-spotted lady-bird," spots 2¹, 3¹, 2^r, 3^r, being present and an extra spot beside 3¹.
36. *H. convergens*; aberr. G₂. "Five-spotted lady-bird," spots 2¹, 3¹, 5¹, 2^r, 3^r, being present.
37. *H. convergens*; aberr. G₃. "Five-spotted lady-bird," spots 2¹, 3¹, 3^r, 6¹, 6^r, being present.
38. *H. convergens*; aberr. H₁. "Four-spotted lady-bird," spots 1¹, 2¹, 1^r, 2^r, being present.
39. *H. convergens*; aberr. H₂. "Four-spotted lady-bird," spots 1¹, 3¹, 1^r, 3^r, being present.
40. *H. convergens*; aberr. H₃. "Four-spotted lady-bird," spots 2¹, 3¹, 2^r, 3^r, being present.
41. *H. convergens*; aberr. I₁. "Two-spotted lady-bird," spots 3¹ and 3^r being present.
42. *H. convergens*; aberr. J₁. "Spotless lady-bird."
43. *H. convergens*; aberr. K₁. "Thirteen-spotted lady-bird," having an additional spot on a line between 1¹ and 4¹. (*Additional*, meaning more spots than the 12 of the mode.)
44. *H. convergens*; aberr. K₂. "Thirteen-spotted lady-bird," having an additional spot between 3^r and 4^r.
45. *H. convergens*; aberr. K₃. "Thirteen-spotted lady-bird," having an additional spot behind 3^r.
46. *H. convergens*; aberr. K₄. "Thirteen-spotted lady-bird," having an additional spot between 2¹ and 3¹.
47. *H. convergens*; aberr. K₅. "Thirteen-spotted lady-bird," having an additional spot in front of 3¹.

48. *H. convergens*; aberr. K₆. "Thirteen-spotted ladybird," having an additional spot between 3¹ and 5¹.
49. *H. convergens*; aberr. K₇. "Thirteen-spotted ladybird," having an additional spot between 3¹ and 4¹.
50. *H. convergens*; aberr. K₈. "Thirteen-spotted ladybird," having an additional spot between 2¹ and 4¹.
51. *H. convergens*; aberr. K₉. "Thirteen-spotted ladybird," having an additional spot between 1¹ and 3¹.
52. *H. convergens*; aberr. K₁₀. "Thirteen-spotted ladybird," having an additional spot behind 3¹.
53. *H. convergens*; aberr. K₁₁. "Thirteen-spotted ladybird," having an additional spot slightly behind a line that would join 2¹ and 3¹.
54. *H. convergens*; aberr. K₁₂. "Thirteen-spotted ladybird," having an additional spot close to front margin.
55. *H. convergens*; aberr. K₁₃. "Thirteen-spotted ladybird," having an additional spot between 1¹ and 2¹.
56. *H. convergens*; aberr. K₁₄. "Thirteen-spotted ladybird," having an additional spot between 5¹ and 6¹.
57. *H. convergens*; aberr. K₁₅. "Thirteen-spotted ladybird," having an additional spot between 3^r and 5^r.
58. *H. convergens*; aberr. K₁₆. "Thirteen-spotted ladybird," having an additional spot between 2^r and 3^r.
59. *H. convergens*; aberr. K₁₇. "Thirteen-spotted ladybird," having an additional spot cephalad of 6^r.
60. *H. convergens*; aberr. K₁₈. "Thirteen-spotted ladybird," having an additional spot cephalad of 5^r.
61. *H. convergens*; aberr. K₁₉. "Thirteen-spotted ladybird," having an additional spot between 2^r and 5^r.
62. *H. convergens*; aberr. L₁. "Fourteen-spotted ladybird," having an additional spot between 1¹ and 2¹, and a second between 4¹ and 6¹.
63. *H. convergens*; aberr. L₂. "Fourteen-spotted ladybird," having one additional spot between 3¹ and 4¹, and a second between 3^r and 4^r.
64. *H. convergens*; aberr. L₃. "Fourteen-spotted ladybird," having one additional spot between 4¹ and 6¹, and a second between 1^r and 3^r.

65. *H. convergens*; aberr. L₄. "Fourteen-spotted lady-bird," having two additional spots between 2¹ and 3¹.
66. *H. convergens*; aberr. L₅. "Fourteen-spotted lady-bird," having one additional spot between 1¹ and 3¹, and a second between 3¹ and 5¹.
67. *H. convergens*; aberr. M₁. "Fifteen-spotted lady-bird," having one additional spot on imaginary line between 3^r and 4^r, a second between 2¹ and 3¹, a third between 4¹ and 6¹.
68. *H. convergens*; aberr. M₂. "Fifteen-spotted lady-bird," having one additional spot between 1¹ and 3¹, a second between 2¹ and 3¹, a third between 2¹ and 4¹.
69. *H. convergens*; aberr. M₃. "Fifteen-spotted lady-bird," having one additional spot between 1¹ and 2¹, a second between 3¹ and 5¹, a third between 2^r and 3^r.
70. *H. convergens*; aberr. M₄. "Fifteen-spotted lady-bird," having one additional spot behind 1¹, a second between 3¹ and 4¹, a third between 3^r and 4^r.
71. *H. convergens*; aberr. M₅. "Fifteen-spotted lady-bird," having one additional spot between 3¹ and 4¹, a second between 2¹ and 4¹, a third on the lateral margin on the right.
72. *H. convergens*; aberr. N₁. "Sixteen-spotted lady-bird," having one additional spot between 2¹ and 3¹, two more in line with 3^r, and a fourth between 1^r and 4^r.
73. *H. convergens*; aberr. O₁. "Seventeen-spotted lady-bird," 1¹ and 1^r being absent and having one additional spot cephalad of 3¹, a second cephalad of 3^r, a third cephalad of 5^r, and four more distributed within the square outlined by 2¹, 3¹, 4¹ and 5¹.
74. *H. convergens*; aberr. P₁. "Eighteen-spotted lady-bird," having two additional spots between 1^r and 3^r, one other between 2^r and 4^r, one other between 2¹ and 4¹, one on an imaginary line between 3¹ and 4¹, and one on an imaginary line between 3¹ and 5¹.
- In another lot of 1,700 individuals collected on October 25, 1902, all together but in another place (in another year) in the neighborhood of Stanford University, examples of 31 of the above described aberrations were present, and in addition specimens representing nine additional aberrations not described above. These new forms are the following:

75. *H. convergens*; aberr. C₂. "Nine-spotted lady-bird," spots 2^r, 3^r and 4^r being absent.

76. *H. convergens*; aberr. C₃. "Nine-spotted lady-bird," spots 1^l, 5^l, 5^r, 6^l and 6^r being absent and an additional spot between 3^r and 4^r and another in front of 3^l being present.

77. *H. convergens*; aberr. D₇. "Eight-spotted lady-bird," spots 5^l, 1^r, 4^r, 5^r, and 6^r being absent and an additional spot between 2^l and 3^l being present.

78. *H. convergens*; aberr. G₄. "Five-spotted lady-bird," spots 2^l, 3^l, 2^r, 3^r and an additional spot near 3^l being present.

79. *H. convergens*; aberr. H₄. "Four-spotted lady-bird," spots 3^l, 3^r, 5^l and 5^r being present.

80. *H. convergens*; aberr. I₂. "Two-spotted lady-bird," spots 1^l and 1^r being present.

81. *H. convergens*; aberr. I₃. "Two-spotted lady-bird," spots 2^l and 2^r being present.

82. *H. convergens*; aberr. L₆. "Fourteen-spotted lady-bird," spots 1^l and 1^r being absent, one additional spot between 1^l and 2^l, two extra spots between 4^r and 5^r, and one between 3^r and 5^r.

83. *H. convergens*; aberr. M₆. "Fifteen-spotted lady-bird," spots 1^l being absent, one extra spot in front of 3^r, two extra spots between 3^l and 5^l and two more between 3^r and 5^r.

This list of "aberrations" is of interest not merely as an illustration of the difficulties that the systematic entomologist (zoölogist) has to face when he undertakes to "refine" his specific descriptions, but as an illustration of the unexpectedly large degree of variation which may be discovered by the careful examination of a considerable series of individuals of a single species. The great dominance of the 12-spotted mode, 90 per cent. of all individuals examined (over 3,000), leads one to find, nine times out of ten, individuals of this species with 12 spots. The species is rightly described as 12-spotted, and the systematist may rest there. But what a revelation to the student of variation! What possibilities for the beginnings of new species if variation in the color pattern is worth while, and capable of being naturally selected!

From a red-brown lady-bird without a black spot to give it pattern or conspicuousness to a lady-bird all dotted over by 18

distinct little black spots is surely a long and pronounced step in pattern development. And every intervening numerical condition is there; two, three, four, five, six, seven, eight, nine, ten, eleven, twelve, thirteen, fourteen, fifteen, sixteen and seventeen spots. But not only are all these discontinuous steps there, but each is produced in from one to eleven ways, *i. e.*, by the various suppression of one or more of the modal twelve, or the various addition of one or more spots to the modal pattern. Natural selection has certainly every traditional opportunity to make new kinds of lady-birds out of *Hippodamia convergens*.

But can natural selection really takes advantage of these conditions? This question brings us finally in the discussion of this case of variation to what is in our minds, the point of by far most interest and significance in the whole matter. It will be recalled that all of the individuals studied were hibernating insects assembled in large numbers. That is they are insects which, hatched in the spring or summer (we do not yet know whether the species is single, or several-brooded in this locality) have undergone their exposed larval and pupal life, and an active adult life from time of issuance from the pupal stage to time of assembling for hibernation. It is a great pity that we do not know exactly how long this time is! The beetles have been exposed however, to the struggle for existence; have competed for food and space; have suffered heat and dryness, and have tested their color pattern for whatever use it exists for. The lady-birds although small are almost all brightly and conspicuously marked and are believed by most naturalists to be inedible (ill-tasting to birds) and to be protected by their bright conspicuous warning color pattern. If so, the color of our hibernating thousands of *Hippodamia* has been put to some test of its usefulness. And all of the hibernating thousands have survived whatever fate may have come to other, to us unknown, thousands. But our variation series are from the saved thousands. *Hippodamia* with no spots, with one spot, with two, three, eight, eleven, fourteen, sixteen, seventeen, eighteen spots have survived the struggle (for a brief or longer period), and have gathered from far and near to

spend the winter in this curious gregarious manner. With spring they will separate, scattering from the safe mountain haunt to the open orchards and fields and gardens of the nearby valley to lay their eggs and then die. The struggle for existence may be severe among the lady-birds; they are surely abundant enough and specialized enough in their food habits to lead one to expect it to be unusually sharp; but it is not sharp enough to make the presence or absence of any particular one or two or half a dozen or dozen or score of black spots on the back a necessary condition to successful life. As far as these observations of the habits and variation status of *Hippodamia convergens* have any worth as a recorded test of the rigor of natural selection they certainly point to a degree of that rigor considerably less than that commonly held and expressed by thorough-going disciples of the *Allmacht* of the natural selection factor in evolution.

It is obvious, of course, that if we could examine a large series of *Hippodamia* individuals in adult condition, but before exposure to the struggle for existence (in this condition), that we should be able to speak more confidently of the exact relation between the color pattern and its life and death selective value to individuals. If no greater (and it is practically beyond possibility for there to be any greater) variation were found to exist among a series of 1,700 individuals with definitive adult pattern taken before exposure to the struggle for life than in a series of 1,700 after such exposure we could say definitively that a variation ranging from none to 18 black spots on the red-brown elytra of this insect (these none to 18 spots being composed of a great many different possible combinations, subtractions from and additions to 12 spots arranged in a certain way, the modal number and arrangement), has no absolute life and death selective value to the individuals and therefore could not offer any "handle" for natural selection. We are trying—so far without success—to obtain a large series of pupæ of *Hippodamia* from which to rear adults unexposed to the struggle for existence.

Variations in Pattern of Pronotum.—The 536 individuals composing the modal subclass 1 of class A, of the series of 1,031

(see p. 259) individuals classified on basis of variations in the elytral pattern were examined and classified on basis of variations in the pattern of the pronotum (dorsal aspect of the prothorax). The modal pattern is formed by the presence of a pair of short

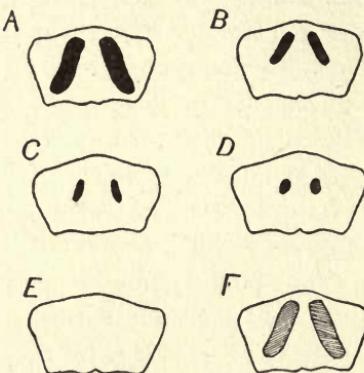


FIG. 48. Diagram showing var. in prothoracic pattern of the convergent lady bird, *Hippodamia convergens*.

white diagonal lines or bars on the red-brown ground color of the pronotum (fig. 48, *A*). These white lines may vary through continuous gradations of shortening and lessening to total disappearance, or may, while retaining their modal size, become shaded or darkened by gradating steps until they are hardly visible as distinct lines or spots at all. The frequencies of the arbitrarily defined classes in this variation are as follows:

Class A: 308 individuals with well-defined white bar-spots (the mode) (fig. 48, *A*). Class B: 168 individuals with the white bar-spots about one half as long and wide (= one half size) as in Class A (fig. 48, *B*). Class C: 31 individuals with the white bar-spots about one third the size of those in Class A (fig. 48, *C*). Class D: 13 individuals with bar-spots reduced to small subcircular spots or points (fig. 48, *D*). Class E: 1 individual with bar-spots actually completely wanting (fig. 48, *F*). Class F: 15 individuals with bar-spots clouded (not white) giving effect of obliteration of marking (fig. 48, *E*).

The frequency polygon for this variation is shown in fig. 49, in which Class F is not represented.

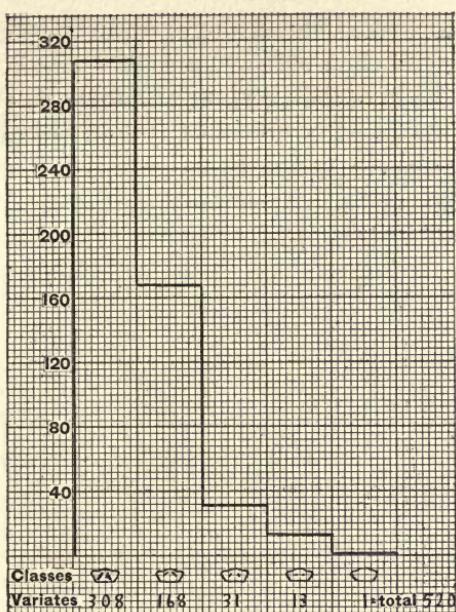


FIG. 49. Frequency polygon of the variation in prothoracic pattern in 521 specimens of the convergent lady-bird, *Hippodamia convergens*, collected at one time and one place.

Thus the mode is one of the extremes of the series of classes (= frequency curve strongly skew), according to the views of Davenport, *et al.*, indicating an evolution of this pattern from the conditions shown in the other cases, or indicating, as held possible by us, a tendency to vary (evolve) in the direction of the other cases.

Variation in Elytral Pattern of *Diabrotica soror* (the flower-Diabrotica).—*Diabrotica soror* is a Chrysomelid beetle which is abundant and a serious pest on the Pacific coast. In its larval stage it lives underground feeding on the roots of alfalfa, chrysanthemum and various other plants; it pupates in a subterranean cell near the surface and the adult beetle on issuance from the pupal cuticle makes its way above ground, and feeds on the buds and opened flowers of roses, chrysanthemums and almost all other garden blossoms. The color pattern of the beetle is definitive and fixed at the time of the first appearance of the adult above ground. The ground color of the elytra is

green with yellowish to bluish tinge, and the large conspicuous dorsal spots, six on each elytron, are pure black.

A lot of 906 individuals, 450 taken October 8, 1901, in a chrysanthemum garden on the Stanford University campus, and the others taken as six small lots from various other places on the campus the same month, were examined and classified on the basis of the obvious variations in the dorsal color pattern caused by the coalescence of various pairs of the large spots. The classes and frequencies are as follows:

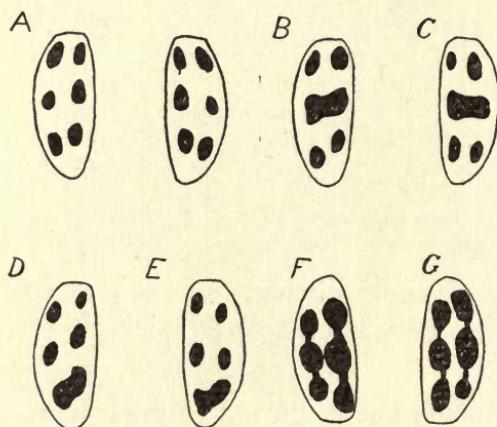


FIG. 50. Diagram showing vars. in elytral pattern of the flower beetle, *Diabrotica soror*.

Class A: 313 individuals have all the spots separate (fig. 50, *A*); this is the condition described for the species and assigned to it in entomological text-books. Class B: 32 individuals with the spots of the middle pair on left elytron confluent (fig. 50, *B*). Class C: 60 individuals with the spots of the middle pair on the right elytron confluent (fig. 50, *C*). Class D: 396 individuals with the spots of the middle pair on each elytron confluent (the mode, fig. 50, *B* and *C*). Class E: 14 individuals with the spots of the posterior pair on the left elytron confluent (fig. 50, *D*). Class F: 17 individuals with the spots of the posterior pair on the right elytron confluent (fig. 50, *E*). Class G: 45 individuals with the spots of the posterior pair on each elytron confluent (fig. 50, *D* and *E*). Class H: 28 individuals with the spots on

left or right elytron or both showing longitudinal confluence (fig. 50, *F* and *G*).

The following frequency polygon represents these frequencies graphically :

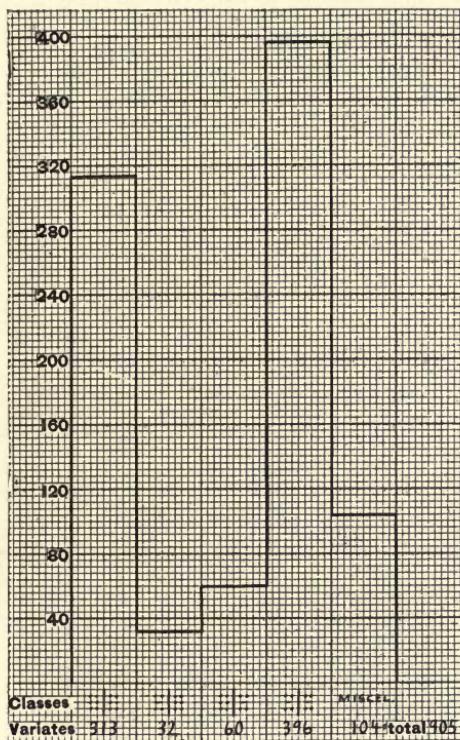


FIG. 51. Frequency polygon of the variation in elytral pattern of 905 specimens of the flower beetle, *Diabrotica soror*, collected at Stanford University, October, 1901.

A second series of 906 individuals was collected just one year later, *i. e.*, October, 1902, from the same chrysanthemum garden that furnished most of the first series (1901) and examined and classified as follows :

Class A : 313 individuals with all spots separate. Class B : 40 individuals with left middle pair confluent. Class C : 55 individuals with right middle pair confluent. Class D : 388 individuals with both middle pairs confluent (the mode). Classes E, F, G and H : 109 individuals with left or right or both

posterior pairs confluent, or with some longitudinal confluence.

These frequencies are graphically shown in the following frequency polygon :

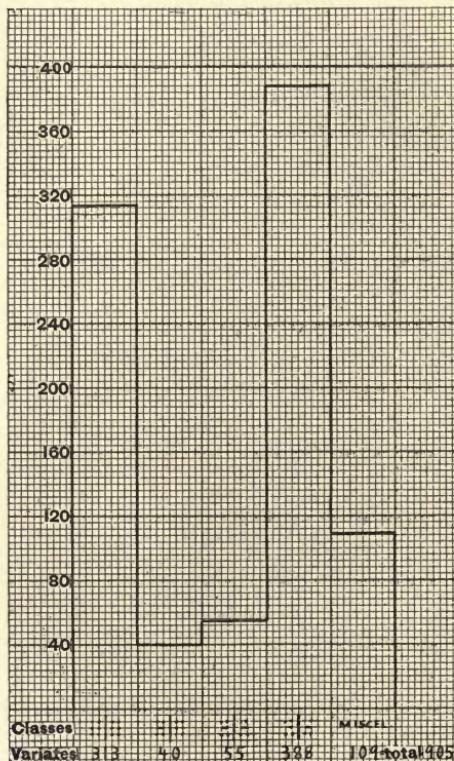


FIG. 52. Frequency polygon of the variation in elytral pattern of 905 specimens of the flower beetle, *Diabrotica soror*, collected at Stanford University, October, 1902.

The similarity of the frequencies in these two lots of 905 individuals each, taken in the same locality at two times just one year apart is striking. The variation in the species in this locality is undoubtedly perfectly fairly shown by a series of 1,000 (app.). To test the value of a smaller series, in the first lot (1901) the following frequencies of the characteristic variations were noted among the first 450 individuals (one half the whole series) examined :

Class A : 134 individuals. Class B : 15 individuals. Class

C: 33 individuals. Class D: 228 individuals. Classes E, F and G: 30 individuals. Class H: 10 individuals.

Comparing this half series of the 1901 individuals with the whole series the percentages of the frequencies of the different variations are as follows:

Class A: 34.5 per cent. in series of 906, 30 per cent. in series of 450. Class B: 3.5 per cent in series of 906, 3.35 per cent. in series of 450. Class C: 6.6 per cent. in series of 906, 7.35 per cent. in series of 450. Class D: 43.7 per cent. in series of 906, 50.6 per cent. in series of 450. Classes E, F and G: 8.4 per cent. in series of 906, 7 per cent. in series of 450. Class H: 3 per cent. in series of 906, 2.25 per cent. in series of 450.

The 1902 series of 905 (app.) individuals is composed of two lots collected in same place, one of about 600 individuals taken October 7, and the other of about 300 individuals taken October 15. Each of these lots classified separately reveals the frequencies of the characteristic variations in nearly identical proportions.

From these examinations of short series there seems to be little doubt that a series of 500 (app.) individuals of *Diabrotica soror* from any locality contains all of the principal variations in the color pattern in proportions representing the actual conditions in the species as it exists in the given locality.

An inspection of the frequency polygons for the series of 1901 and 1902 shows that the color pattern condition accepted by entomologists (on a basis of the original description of the species and repeated references to the pattern in the literature of coleopterology) as diagnostic of the species is only one of two modal color pattern conditions and is indeed the less frequent one of the two. There are more flower *Diabroticas* with four distinct black spots and a central transverse band (made by the confluence of a pair of spots) on each elytron than there are individuals with six distinct spots on each elytron. Which is *soror*? According to the views of the Pearson, Davenport, *et al.*, school of variation students, this bimodal frequency curve of *D. soror* indicates a tendency toward the splitting of one species into two, a beginning in the formation of a new species. In the

light of this interpretation of the variation conditions of *soror* it would be of much interest if we could know the exact (as determined by statistical study) conditions of the species at the time *soror* was originally described. Was the 12-free-spots-condition really the dominant mode then? Or did the original describer simply have a few specimens in hand, all of which happened to be of this type? Fortunately we are able to present the statistical facts of this color pattern variation in a series of 906 individuals of *soror* collected on the Stanford University campus in 1895 (a collections lot found by us in rummaging through the old unworked material in the department's cabinets). The characteristic color-pattern variations in this lot are the same as in the 1901 and 1902 lots, with the following frequencies:

Class A: 383 individuals with all twelve spots separate (the mode). Class B: 55 individuals with left middle pair confluent. Class C: 64 individuals with right middle pair confluent. Class D: 203 individuals with both middle pairs confluent. Class E: 11 individuals with left posterior pair confluent. Class F: 8 individuals with right posterior pair confluent. Class G: 26 individuals with both posterior pairs confluent. Class X: 47 individuals with both middle and posterior pairs of both sides confluent. Class H: 108 individuals showing longitudinal confluence on one or both sides.

The polygon showing these frequencies graphically is as shown on next page.

Thus in 1895, seven years ago, *soror* in the same locality, showed a dominant pattern of twelve free spots on the elytra (fig. 50 A), as originally described for the species. But the pattern second in point of frequency was that which to-day is the dominant one in the species (fig. 50 B, C). The percentages of these two patterns in the three series collected in 1895, 1901 and 1902 from same locality are:

With all spots free: 42.35 per cent. in series of 1895, 34.5 per cent. in series of 1901, 34.5 per cent. in series of 1902.

With spots of middle pairs fused: 22.4 per cent. in series of 1895, 43.7 per cent. in series of 1901, 42.8 per cent. in series of 1902.

The new species of *Diabrotica*, splitting away from *D. soror*

and only one half as abundant as the typical *soror* in 1895, is now (1901, 1902) two thirds as abundant.*

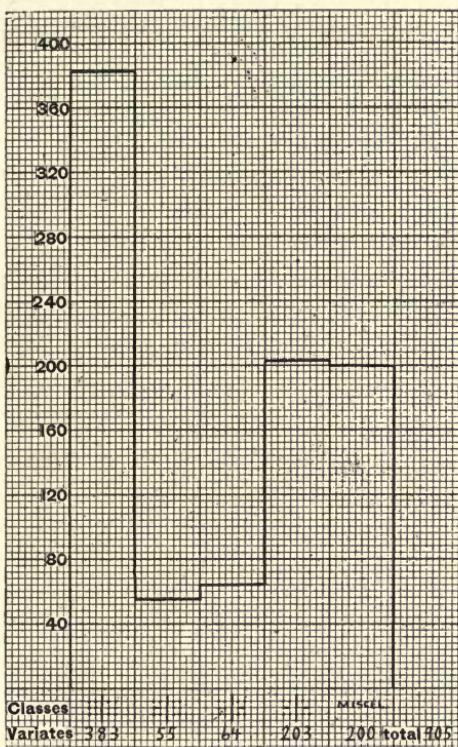


FIG. 53. Frequency polygon of the variation in elytral pattern of 905 specimens of the flower beetle, *Diabrotica soror*, collected at Stanford University, 1895.

A pertinent question in this connection is that touching the cause of this increasing frequency of a certain variation in this species. Is the form with both middle spots fusing to form a broad transverse bar being naturally selected? Or, in the light of our observations of *Hippodamia* with its great variety of color pattern among individuals exposed for a season to the struggle for existence, are we not to consider seriously the possibility of the condition in *Diabrotica* being brought about by

* Since this paper went to press, 905 individuals of *D. soror*, collected Oct., 1904 from same locality as series of 1895, 1901 and 2, show the following percentages of the various patterns: 20.9 with all twelve spots separate; 65.4 with spots of middle pairs fused; 13.5 with miscellaneous patterns.

determinate variation, the condition being the result of a tendency in the species, produced by certain to us unknown extrinsic or intrinsic influences, not selective or purposeful? To our mind this color pattern variation, any more than that in *Hippodamia*, is not to be looked on as sufficient basis for a life and death selection. Where it takes close examination by our trained eyes, often aided by the simple lens, to distinguish the exact character of the variation, is a beetle to lose or save its life by the relation of this variation to the eyes of swooping birds or darting predaceous insects (which, with toads and lizards, are almost the only external selective agencies with which the color pattern has to do)? Predaceous insects do not see slight differences in pattern, at least at any range beyond a few centimeters. They discover their prey by the visual perception of its movements, and by their keen sense of smell. Birds do not distinguish protectively colored insects; but shall *soror* individuals with two spots each a millimeter in diameter, fused, held to be more safely colored than *soror* individuals with these two spots separated by a hair's breadth? But that, it seems to us, is the necessary admission if natural selection is to be looked on as the only factor, outside of purely fortuitous variation, in the gradually changing character of the color pattern of *soror*.

It will be of interest to note the condition of variation in certain lots of *soror* all collected in October, 1902, at various localities in California other than the Stanford campus. We wished to discover if *soror* throughout its range shows this same tendency toward the production of a dominant variety of the type of class D (in the Stanford series). We were able to obtain several (usually small) series from a few distant localities, covering, however, only a small part of the range of the species. We hope to add gradually to this series of geographically scattered lots.

A lot of 405 individuals from Santa Rosa, California (about sixty miles from Standford campus), shows variation frequencies as follows:

Class A: 228 individuals, with all spots free. Class B: 105 individuals with both middle pairs fused. Class C: 12 individuals with left middle pair fused. Class D: 18 individuals with

right midde pair fused; 42 individuals showing other miscellaneous variation.

A lot of 224 individuals from two miles east of Mountain View, California (nine miles from Stanford campus), shows variation frequencies as follows:

Class A: 130 individuals, with all spots free. Class B: 28 individuals, with both middle pairs fused. Classes C and D: 23 individuals, with middle pair on either right or left side fused; 43 individuals, miscellaneous.

A lot of 145 individuals from Oakland, California (40 miles from Stanford campus), shows variation frequencies as follows:

Class A: 49 individuals, with all spots free. Class B: 61 individuals, with both middle pairs fused. Classes C and D: 14 individuals, with either right or middle pair fused; 21 individuals, miscellaneous.

A lot of 72 specimens from Arcata, California (200, approximately, miles from Stanford campus) shows variation frequencies as follows:

Class A: 7 individuals, with all spots free. Class B: 47 individuals with both middle pairs fused. Class C: 6 individuals, with left middle pair fused. Class D: 8 individuals, with right middle pair fused; 54 individuals, miscellaneous.

A lot of 103 individuals from Steven's Creek, California, (15 miles from Stanford campus), shows the following variation frequencies:

Class A: 59 individuals, with all spots free. Class B: 22 individuals, with both middle pairs fused. Classes C and D: 11 individuals, with either left or right middle pair fused; 11 individuals, miscellaneous.

A lot of 149 individuals from Menlo Park, California (2 miles from Stanford campus), shows variation frequencies as follows:

Class A: 49 individuals, with all spots free. Class B: 78 individuals, with both middle pairs fused. Class C: 6 individuals with left middle pair fused. Class D: 3 individuals with right middle pair fused; 13 individuals, miscellaneous.

A lot of 26 individuals from Pacific Grove, California, 90 miles from Stanford campus, shows the following variation frequencies:

Class A: 7 individuals, with all spots free. Class B: 9

individuals, with both middle pairs fused. Class C: 3 individuals, with left middle pair fused. Class D: 3 individuals, with right middle pair fused; 4 individuals, miscellaneous.

While most of these lots are small and therefore are not necessarily (although possibly) fair indicators of the actual condition of the variation frequencies of the species in the given locality, they do pretty certainly show that the condition existing in the species at Stanford, namely, a dominance of the variety with both middle pairs of spots fused, does not exist throughout the range of the species. For example, in the series of 405 individuals from Santa Rosa the 12-spots-free form occurs twice as often as the form with middle pairs fused. Dominance or modality of the form with all spots free is also shown by the series from Mountain View, and that from Stevens Creek. On the contrary the condition shown by the Stanford series is also shown by the lot from Oakland, lot from Arcata, that from Menlo Park and the very small lot from Pacific Grove. What significance these conditions have for us is obviously not clear. But they indicate that if natural selection is determining the dominance of the form with fused spot at Stanford, the agents in this selection (in as far as the selection is actually based on the color pattern) which can hardly be any others than birds, toads, lizards, predaceous and parasitic insects, show curiously different eyesight in different localities in California. On the other hand it is quite as obvious that these varying conditions of dominance throw no light on the causal factors in what we have called the determinate variation of the species. If these factors at Stanford induce a variation tending toward fusion of the spots, such factors must be assumed to be much less effective at Santa Rosa, 75 miles away. We can only say that our belief in the unknown factors of variation (which comes to saying, the unknown factor in evolution) is only strengthened by the anomalous conditions shown by the variation in these scattered lots of *Diabrotica soror*.

Variation in the Abdominal and Face Markings of *Vespa* sp. (Yellow Jacket).—In a lot of 496 individuals of *Vespa* sp., a yellow jacket, collected in October and November, 1901, at

various places on the campus of Stanford University, a considerable variation in the black patterning on the yellow ground of the dorsal surface of the abdominal segments was noted.. The yellow jackets are insects of complete metamorphosis, the colors and patterns of the adults (imagines) appearing in definitive and unchangeable condition immediately on the expanding and drying of the legs, wings and body-wall, after issuance from the pupal cuticle. The wasps are well-defended insects by reason of their sting, and the conspicuous black and yellow colors in banded pattern are usually looked on as of the nature of warning colors. If so their condition is due in some or large degree to the action of natural selection, and variations in the pattern are to be looked on as advantageous or disadvantageous.

We have arranged the 496 individuals of the lot into six principal classes based on the variation in the black markings on the dorsum of abdominal segment 2, and inside of these six into ten other classes based on the variations in the black markings on the dorsum of abdominal segment 5. These classes are as follows :

Class A: 71 individuals with both black spots of segment 2 free from anterior black transverse bar (fig. 54, *A*). Subclass Aa: 40 (of Class A) have the corresponding two spots of segment 5 attached (fig. 54, *Aa*). Subclass Ab: 8 have both of them free (fig. 54, *Ab*). Subclass Ac: 3 have the right spot free and the left attached (fig. 54, *Ac*). Subclass Ad: 2 have the left spot free and the right attached (fig. 54, *Ad*). (In 18 individuals we could not make out the condition on segment 5 without breaking up the dried specimens.)

Class B: 22 individuals with the left spot of segment 2 attached and the right one free (fig. 54, *B*). Subclass Ba: 13 have both the spots of segment 5 attached (fig. 54, *Ba*). Subclass Bb: 1 has both of these spots free (fig. 54, *Bb*). (In 8 individuals we could not make out the condition on segment 5 without breaking up the dried specimens.)

Class C: 7 individuals with the right spot of segment 2 attached, the left one free (fig. 54, *C*). Subclass Ca: 6 have both the spots of segment 5 attached (fig. 54, *Ca*). Subclass Cb: 1 has both of these spots free (fig. 54, *Cb*).

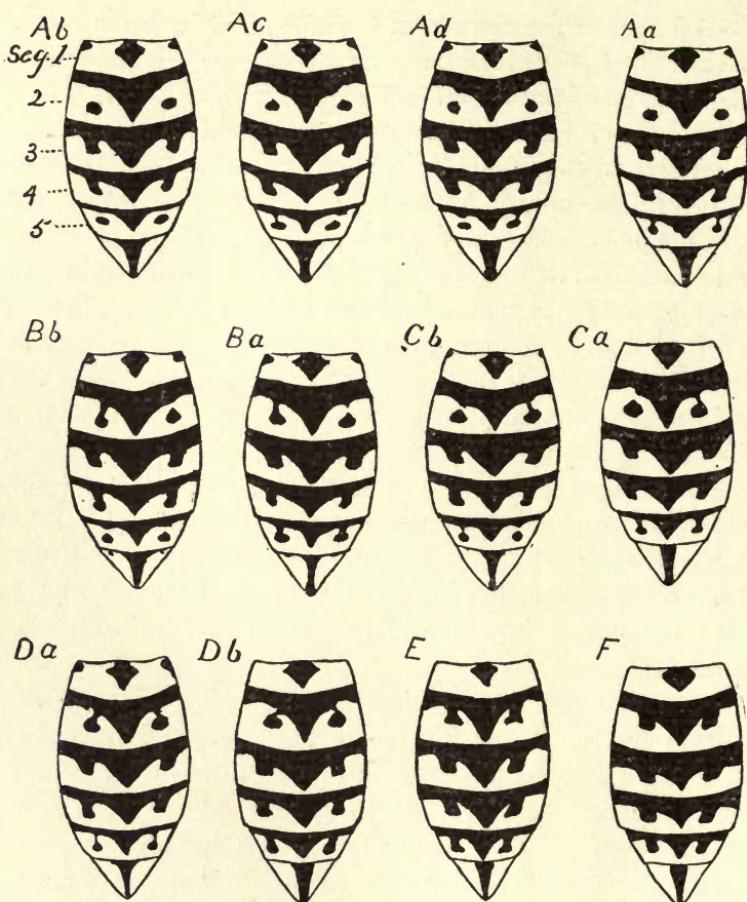


FIG. 54. Diagram showing var. in pattern in the abdominal segments of the yellow jacket, *Vespa* sp.

Class D: 41 individuals with both spots of segment 2 attached by a very narrow stem (mere line) (fig. 54, *D*); of which all have both spots of segment 5 attached. Subclass Da: 11 individuals have one or both spots of segment 5 attached by a narrow stem (fig. 54, *Da*). Subclass Db: 22 individuals have both spots attached by a broad stem or bar (fig. 54, *Db*).

Class E: 201 individuals with both spots of segment 2 attached by a broad stem, but the ends, *i. e.*, spots, are buttoned, *i. e.*, are slightly broader than the stem (fig. 54, *E*). All these individuals have both spots of segment 5 attached.

Class F: 154 individuals with both spots of segment 2 with their attaching stems reduced to mere short broad bars tending to be wider at base (attachment) than at free end (fig. 54, *F*). All these individuals have both spots of segment 5 attached.

From this rough grouping it is obvious that the modal, or most usual pattern is one in which both spots of segment 2 and both of segment 5 are attached. From this condition to that in which both are free in both segments, there is a perfectly continuous series of gradations. Indeed the characteristic thing about this case of pattern variation is its perfect exemplification of typical continuous variation, the connecting of its extremes by perfect series of almost insensibly slight gradations.

The pattern of the frons of the head of another, smaller lot of 238 individuals of the same species of *Vespa* was examined for variation. The specimens have been divided into four classes as follows:

Class A: 137 individuals with a single central free spot (fig. 55, *A*).

Class B: 64 individuals with the spot attached by a narrow stem (fig. 55, *B*).

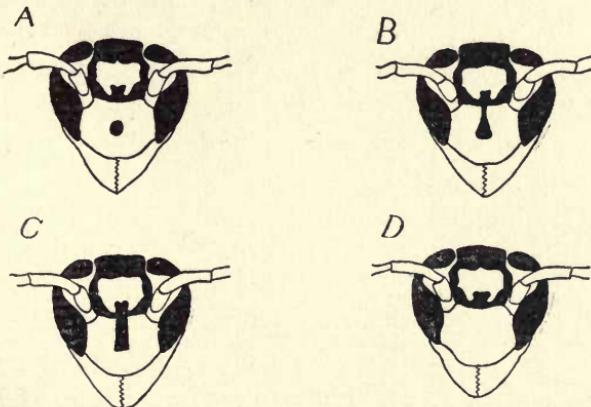


FIG. 55. Diagram showing var. in pattern of frons of the yellow jacket, *Vespa* sp.

Class C: 34 individuals with the spot attached by a broad stem so that stem and spot usually form a short broad bar of nearly uniform width (fig. 55, *C*).

Class D: 3 individuals with no spot or stem (fig. 55, *D*).

This variation also is perfectly continuous, every possible (visible) gradation between a distinct spot at some distance from the upper cross band and the broad, short vertical bar, ranging through a distinct spot connected by the barest thread-line, a spot connected by a thicker line and so on to the short bar no wider at its free (spot) end than at its middle.

To ascertain if any correlation exists between the variation in the face marking and that in the abdominal pattern, the lot of 496 individuals examined and arranged in respect to abdominal pattern was also arranged within the classes established on a basis of variation in abdominal pattern, on a basis of variation in face markings, with the following result:

Class A : 71 individuals with both black spots of abdominal segment 2 free from anterior black transverse bar (fig. 54, *A*). Subclass 1 : 46 (of Class A) have the face spot free and subcircular (fig. 55, *A*).

Subclass 2 : 4 (of Class A) have the face spot free but elongated and nearly attached. Subclass 3 : 19 (of Class A) have the face spot narrowly attached (fig. 55, *B*). Subclass 4 : 1 (of Class A) has the face spot broadly attached (fig. 55, *C*).

Class B : 22 individuals with the left spot of abdominal segment 2 free and the right one attached (fig. 54, *B*). Subclass 1 : 10 (of Class B) have the face spot free and subcircular (fig. 55, *A*). Subclass 2 : 2 (of Class B) have the face spot elongated and nearly attached. Subclass 3 : 8 (of Class B) have the face spot narrowly attached (fig. 55, *B*).

Class C : 7 individuals with the right spot of abdominal segment 2 attached, the left one free (fig. 54, *C*). Subclass 1 : 6 (of Class C) have the face spot free (fig. 55, *A*). Subclass 2 : 1 (of Class C) has the face spot narrowly attached (fig. 55, *B*).

Class D : 41 individuals with both spots of abdominal segment 2 attached by a very narrow stem (mere line) (fig. 54, *D*), of which all have both spots of abdominal segment 5 attached, either by a narrow or broad line. Subclass 1 : 20 (of Class D) have the face spot free and subcircular (fig. 55, *A*). Subclass 2 : 1 (of Class D) has the face spot elongated and nearly attached. Subclass 3 : 20 (of Class D) have the face spot narrowly attached (fig. 55, *B*).

Class E: 201 individuals with both spots of abdominal segment 2 attached by a broad stem, but the ends, *i. e.*, spots are buttoned, *i. e.*, are slightly broader than the stem (fig. 54, *E*); all these individuals have both spots of abdominal segment 5 attached. Subclass 1: 89 (of Class E) have the face spot free and subcircular (fig. 55, *A*). Subclass 2: 28 (of Class E) have the face spot elongated and nearly attached. Subclass 3: 78 (of Class E) have the face spot narrowly attached (fig. 55, *B*). Subclass 4: 7 (of Class E) have the face spot broadly attached (fig. 55, *C*).

Class F: 154 individuals with both spots of segment 2 with their attaching stems reduced to mere short broad bars tending to be wider at base (attachment) than at free end (fig. 54, *F*); all these individuals have both spots of segment 5 attached. Subclass 1: 69 (of Class F) have the face spot free and subcircular (fig. 55, *A*). Subclass 2: 12 (of Class F) have the face spot elongated and nearly attached. Subclass 3: 60 (of Class F) have the face spot narrowly attached (fig. 55, *B*). Subclass 4: 10 (of Class F) have the face spot broadly attached (fig. 55, *C*).

From an inspection of the above there actually seems to be an indicated tendency for the spot in the face to be free when the abdominal spots are free, and for this spot to be attached or fused with the transverse bar above it when the abdominal spots are fused with their corresponding transverse bars. But this is not at all emphasized, being indeed plainly obvious in the case of Class A when compared with any other class, but not when any two of these other classes are compared with each other.

Variations in the Prothoracic Pattern of *Tettigonia* sp. (Leaf Hopper).—The Typhlocybinæ, leaf hoppers, are small, usually greenish, insects of the family Jassidæ, order Hemiptera, common in pastures, vineyards, etc., where they feed on the sap of the green leaves of the growing plants. They occur sometimes in countless numbers, and may do much damage. A lot of 221 individuals of *Tettigonia* sp. collected on one day on the campus of Stanford University was examined and classified by us on the basis of the variations in the number and disposition of the members of a series of small black spots lying just behind

the anterior margin of the pronotum. From an examination of this series of spots in many individuals we found ourselves able to describe the variation in these spots most conveniently by assuming the normal condition of the series to be that in which it would be composed of nine spots, one in the center and four symmetrically disposed on each side (fig. 56). This arrangement together with the relative size of the spots and the distinguishing numbers assigned them are all shown in fig. 56. As a matter of fact this hypothetical normal was not found to exist in a single individual; instead of normal therefore we may call

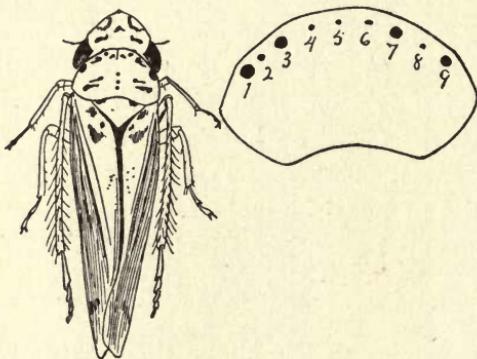


FIG. 56. The leaf hopper, *Typhlocyba comes*, and diagram showing hypothetical, symmetrical arrangement of spots along the cephalic margin of the prothorax.

it the "condition of symmetry," an ideal condition not existent in any of the specimens examined.

These insects have an incomplete metamorphosis and this prothoracic pattern is exposed to be tested for usefulness or to be modified by direct reaction to environment throughout the immature life of the leaf hoppers, which life is the same as regards food and most other relations to the external world as that of the adult and is spent in the same environment. The various classes of variation of these prothoracic spot markings and the frequencies of these classes are as follows: 1 individual has an added spot beyond¹ 4¹; 2 individuals have an added spot beyond 4¹, and 4^r; 1 individual has an added spot beyond

¹Spots 1^l, 2^l, 3^l and 4^l are spots 1, 2, 3 and 4 of fig. 56, while spots 1^r, 2^r, 3^r and 4^r are spots 9, 8, 7 and 6, respectively of fig. 56: spot 0 is spot 5 of fig. 56.

4^1 and o is a line (not a spot); 1 individual has an added spot beyond 4^1 , and $2^1 + 3^1$ and $2^r + 3^r$ are confluent; 1 individual has an added spot beyond 4^1 , and 4^r , and $2^1 + 3^1$ are confluent; 1 individual has an added spot beyond 4^1 , and 4^r , and lacks 3^r and 3^1 ; 1 individual has an added spot beyond 4^1 , and 4^r , and lacks 3^1 , 3^r and o; 1 individual has an added spot beyond 4^1 , lacks 1^r , and has $3^r + 2^r$ confluent; 1 individual has an added spot beyond 4^1 , lacks 3^r , and has o a line; 2 individuals have an added spot beyond 4^1 , and lack 3^1 , 3^r , 2^1 and 2^r ; 2 individuals have an added spot beyond 4^r , and lack 3^1 , 3^r , 1^1 , 1^r and o; 1 individual has an added spot beyond 4^r and lacks 3^1 ; 2 individuals have an added spot beyond 4^r and lack 3^1 and 3^r ; 1 individual has an added spot beyond 4^r , and has $2^1 + 3^1$ confluent; 1 individual has an added spot beyond 4^r , and has $2^1 + 3^1$, and $2^r + 3^r$ confluent; 1 individual has an added spot in front of 1^1 and of 2^1 and lacks 3^1 and 3^r ; 1 individual has an added spot near 1^1 and lacks o; 4 individuals have $2^r + 3^r$ confluent; 8 individuals have $2^1 + 3^1$ confluent; 17 individuals have $2^1 + 3^1$ and $2^r + 3^r$ confluent; 2 individuals have $2^r + 3^r$ confluent and o a line; 3 individuals have $3^1 + 3^1$ and $2^r + 3^r$ confluent, and o a line; 4 individuals have all spots present, o being a line; 4 individuals have 3^r lacking; 1 individual has 1^r lacking; 6 individuals have 3^1 lacking; 22 individuals have 3^1 and 3^r lacking; 3 individuals have 1^1 and 1^r lacking; 8 individuals have 3^1 , 3^r and 1^r lacking; 5 individuals have 3^1 , 3^r and 1^1 lacking; 2 individuals have 3^1 and 1^r lacking; 2 individuals have 1^1 , 1^r and 3^1 lacking; 3 individuals have 1^1 , 1^r and 3^r lacking; 3 individuals have 3^1 , 3^r and o lacking; 1 individual has 4^1 , 3^r and 1^r lacking; 1 individual has 3^1 , 3^r , 1^1 and o lacking; 1 individual has 1^1 , 1^r , 4^1 and 3^r lacking; 4 individuals have 1^1 , 1^r , 3^1 and o lacking; 44 individuals have 1^1 , 1^r , 3^1 and 3^r lacking; 22 individuals have 1^1 , 1^r , 3^1 , 3^r and o lacking; 1 individual has 1^1 , 1^r , 3^1 , 3^r , 4^r and o lacking; 1 individual has 1^1 , 1^r , 3^1 , 3^r , 4^1 , and o lacking; 1 individual has 1^r lacking and $2^r + 3^r$ confluent; 1 individual has 1^r lacking and $2^1 + 3^1$, $2^r + 3^r$ confluent; 1 individual has o lacking and $2^1 + 3^1$, $2^r + 3^r$ confluent; 1 individual has 1^1 lacking and $2^r + 3^r$ confluent; 1 individual has 1^1 , 1^r and 3^1 lacking and $2^r + 3^r$ confluent; 1 individual has 3^r and o lacking and $2^1 + 3^1$

confluent; 1 individual has 1^l and 1^r lacking and $2^r + 3^r$ confluent; 1 individual has 2^r and 3^r lacking and $2^l + 3^l$ confluent; 1 individual has 1^l and 1^r lacking and $2^l + 3^l$ confluent; 1 individual has 1^l 1^r , 3^l and o lacking and $2^r + 3^r$ confluent; 2 individuals have 1^l lacking and $2^r + 3^r$ and $2^l + 3^l$ confluent; 2 individuals have 1^l and 3^l lacking and $2^r + 3^r$ confluent; 3 individuals have 1^l and 1^r lacking and $2^r + 3^r$ and $2^l + 3^l$ confluent; 1 individual has 3^l lacking and o a line; 1 individual has 1^l , 1^r and 3^r lacking and o a line; 2 individuals have 3^l and 3^r lacking and o a line; 4 individuals have 1^l , 1^r , 3^l and 3^r lacking and o a line; 1 individual has 1^l , 1^r , 3^r and o dim and 3^l shifted toward 4.

The variation in the number and disposition of these prothoracic spots consists, as may be noted from an inspection of the above table, of the addition (never more than two spots) or subtraction (never more than five spots) of spots; of the coalescence of two adjoining spots on either or both sides; of the substitution of a small line for the spot o (spot 5, fig. 56) in the middle of the series; and of many combinations of any two or several of these conditions. The modal condition is that when the series is composed of five spots, a middle one (o), with two on each side (2^l , 4^l and 2^r , 4^r respectively). The next most frequent conditions are when the series consists of but four spots (the middle spot, o, of the modal condition being absent), and when the series consists of seven spots, namely the middle one (o) and three on each side (1^l , 2^l , 4^l and 1^r , 2^r , 4^r). Another frequent condition is when all nine spots (of the hypothetical condition of symmetry) are present with two on each side ($2^l + 3^l$ and $2^r + 3^r$ respectively) confluent or fused. The remaining fifty-six conditions of this prothoracic series of spots as noted in the lot of 221 individuals are represented by from one to eight cases each. That these variations can have a life and death selective worth seems inconceivable to us, and yet they are of the general character on which new species (in the teeming genera of insects) are established. That such diverse conditions of this prothoracic pattern have survived through their immature life until the insects have reached maturity is evidence incontrovertible that the selective agents have overlooked as

many variations as remain. This pattern has during all this life or at least during most of it, been as effective as it may be in helping or hindering the individual to successful life.

Variation in Prothoracic Markings of a Flower-bug.—Three hundred and seventy-eight individuals of a flower-bug (sp. undetermined), collected at one time by sweeping the net over a few rods of alfalfa and *Baccharis* on the campus of Stanford University were examined for variation in the number and arrangement of the spots constituting the pattern of the pronotum. This insect belongs to the family Capsidæ, order Hemiptera, and has an incomplete metamorphosis.

The series of specimens has been grouped in sixteen classes as follows (the spots have been given numbers for the sake of referring to them readily, see diagram, fig. 57).

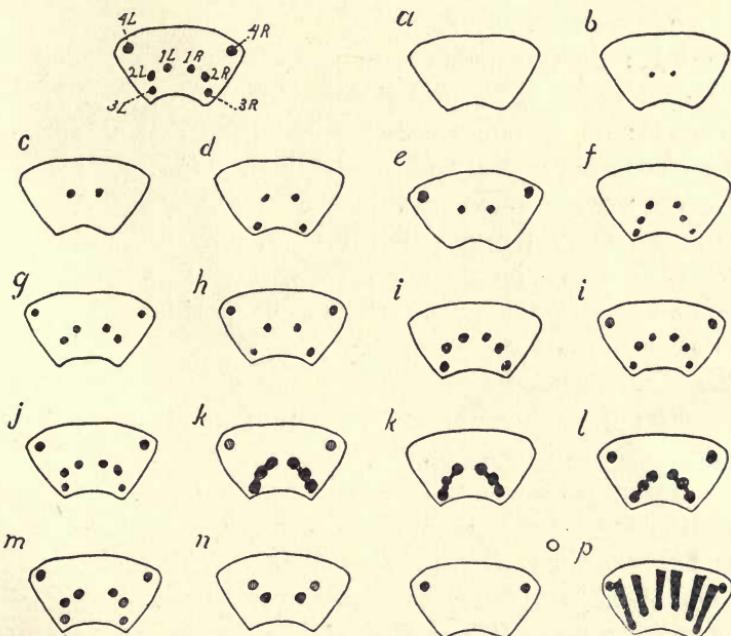


FIG. 57. Diagram showing variation in pattern of the prothorax of a flower-bug.

Class A: 2 specimens without spots (fig. 57, *a*).

Class B: 36 specimens with spots r^l and r^r present, but small (fig. 57, *b*).

Class C: 129 specimens with spots 1^l and 1^r well defined (fig. 57, c).

Class D: 5 specimens with spots 1^l , 1^r , 3^l and 3^r present (fig. 57, d).

Class E: 24 specimens with spots 1^l , 1^r , 4^l and 4^r present (fig. 57, e).

Class F: 7 specimens with spots 1^l , 1^r present and 2^l 2^r , 3^l and 3^r dimly indicated (fig. 57, f).

Class G: 16 specimens with spots 1^l , 1^r , 2^l , 2^r , 4^l and 4^r present (fig. 57, g).

Class H: 2 specimens with spots 1^l , 1^r , 3^l , 3^r 4^l and 4^r present (fig. 57, h).

Class I: 17 specimens with spots 1^l , 1^r , 2^l , 2^r , 3^l and 3^r present and 4^l , 4^r , dim or absent (fig. 57, i, i').

Class J: 43 specimens with spots 1^l , 1^r , 2^l , 1^r , 3^l , 3^r , 4^l and 4^r well defined (fig. 57, j).

Class K: 20 specimens with spots 1^l , 2^l and 3^l and 1^r , 2^r and 3^r coalescent and 4^l and 4^r dim or absent (fig. 57, k, k').

Class L: 68 specimens with spots 1^l , 2^l and 3^l and 1^r , 2^r and 3^r coalescent and 4^l and 4^r well defined (fig. 57, l).

Class M: 1 specimen with spots 1^l , 1^r , 2^r , 4^l and 4^r well defined and with 2^l , 3^l and 3^r dim (fig. 57, m).

Class N: 4 specimens with spots 1^l and 1^r present and an additional dim spot between 1^l and the position of 4^l , and 1^r and the position of 4^r (fig. 57, n).

Class O: specimens with spots 4^l and 4^r present (fig. 57, o).

Class P: 3 specimens showing strong tendency to longitudinal markings (fig. 57, p).

The variations seem to cover most of the possible combinations afforded by the possibilities of any one or more of eight spots being absent, dim, or well defined. The bilateral correlation of the variations is pronounced; indeed there is but one exception noted (Class M). The mode is the presence of spots 1 and 1 alone, but well defined (Class C; Class B is really but a subdivision of the mode). Next to the modal class comes that in which all the spots are present, with three on each side coalesced to form a diagonal line (Class L; Class K is also but a subdivision of this next to the modal class). Third

largest is that condition in which all the spots are present, distinct and well defined (Class J; Class I is partly only a subdivision of Class J). From the series it is apparently not possible to suggest the probable tendency of the pattern's evolution; perhaps a larger series would throw more light on the matter. The strikingly large range and pronounced character of the variations in this short series of specimens cannot but be interesting and suggestive to students of the significance of variations.

Variations in the Prothoracic Pattern of *Corisa* sp. (Water-boatman). — The Corisidæ, water-boatmen, are aquatic Hemiptera, common in all fresh-water ponds and stream pools. The back is patterned by fine lines, more or less wavy, of pale color on a dark ground so as to produce the impression of a fine mottling. The combination of color and patterning is such as, without doubt, to make the insect very inconspicuous in the water. Indeed to the limited vision of its enemies, such as other predaceous aquatic insects, fishes, etc., it ought to be nearly indistinguishable when at rest, and thus only betrayed by its movements. The pattern on the dorsum of the prothorax consists of (usually) thirteen or fourteen fine transverse lines (fig. 58). The variation in the number of these lines was determined in a lot of 502 individuals taken by a single sweep of the collecting net from a pond on the Stanford University campus. These insects have an incomplete metamorphosis and in their development from young to adult, exposed for this whole time to the direct influence of the environment which usually remains that of the whole adult life as well, they undergo whatever changes take place between their condition at time of hatching and that at maturity. The advantage or worth of the color-pattern is indeed constantly subjected to test during the whole life after hatching.

The classes of variation in number and character of these lines constituting the prothoracic pattern, and their frequencies

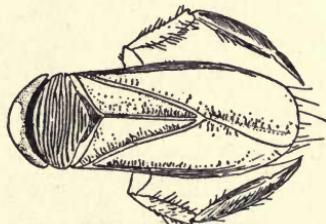


FIG. 58. The water boatman, *Corisa* sp., showing transverse wavy lines forming the prothoracic pattern.

in the 502 individuals taken from the same spot at the same time are as follows: 22 individuals have 16 lines; 63 individuals have 15 lines; 172 individuals have 14 lines; 146 individuals have 13 lines; 55 individuals have 12 lines; 28 individuals have 11 lines; 21 individuals have the lines too much interrupted to be counted; 8 individuals have the lines too much netted, *i. e.*, connected with each other, to be counted; 7 individuals have the lines too much interrupted and netted to be counted.

As indicated in the description of three classes in the foregoing table, the lines show variations in degree of distinctness, tendency toward coalescence, and tendency toward interruptions or breaks in continuity. In some instances the lines are distinct and nearly parallel. In most cases a tendency toward coalescence of the lines is manifest, a wide range in the specific character of this coalescence being present. Two or more lines may coalesce in the middle or at one or both ends. In some cases a network is thus formed and it becomes difficult or really impossible to count the lines. In some cases the lines are wavy, and along the posterior margin the lines are frequently connected by irregular markings resembling those on the wings. Interruption or obliteration of parts of the lines also occurs and in a few cases certain lines are farther apart than in others. In some specimens more or less regular, elongated spots occur, one on each side near the median line half way between anterior and posterior margins. They appear at first sight to be simply interruptions of the transverse lines, but in some instances the latter may be traced through the spots when the specimens are held in proper light.

Altogether the variation appears to follow pretty fairly the law of error, the modal number of lines being 14 with 13 nearly as frequent. The pattern is almost certainly distinctly protective in character and maintained in its present condition by the action of natural selection. The residue of variation, here tabulated, is composed of characters evidently not of selective value. It would indeed seem reasonable to expect that a variation of but two or three lines on either side of the mode would not seriously invalidate the protecting (water mimicry) value of the pattern. Thus in this case where the pattern is obviously of direct pro-

tective value, no wide range of variation among adult individuals (that is, those exposed to the rigor of selection) obtains.

Variation in the Eye-spots on wings of *Parnassius smintheus* and *Cœnonympha galactinus* (Butterflies). — Butterflies have a complete metamorphosis, the wing-pattern appearing in its definitive condition at the time of the first activity (free flight) of the adult insect (imago). The colors and pattern are produced by scales, the color depending on pigment contained in the scales (reds, browns, etc.,) or on their structure, consisting of superposed transparent lamellæ, and parallel, microscopically adjacent, ridges or striæ (metallic blues, greens, purples, etc.). The scales are dead structures when the wings are once fully expanded and dried, so that the color-pattern is congenital, *i. e.*, not acquired by reaction during the life-time of the adult to environmental chromatic conditions.

In a lot of 60 adult individuals of *Cœnonympha galactinus*



FIG. 59. The Parnassian butterfly, *Parnassius smintheus*, showing eye-spots on wings.

collected at various times and places near Stanford University, the small ocelli or eye-spots which occur on the under sides of the fore and hind wings were found to vary as follows: In males, from no spot to two distinct spots on fore wings, and from one incomplete spot to one incomplete and three complete spots on the hind wings. In females, from no spot to one complete and one incomplete spot on fore wings, and from one incomplete spot to one incomplete and two complete spots on hind wings.

In a lot of 16 males and 6 females of *Parnassius smintheus* collected in one summer in Estes Park, Colorado, the following conditions of the wing ocelli (fig. 59) were found:

In the males, 14 individuals had three complete red-centered ocelli on the under side of the hind wings, while two individuals had but two such ocelli.

In the six females the red-centered ocelli on the upper side of the hind wings varied in number from two to four.

These two cases are only included as examples of a condition familiar to all collectors and systematic students of moths and butterflies, namely, the constant presence of considerable variations in the wing-patterns. As these patterns are certainly to be looked on as blastogenic characters, and as positive usefulness must certainly be presumed in connection with so spec-

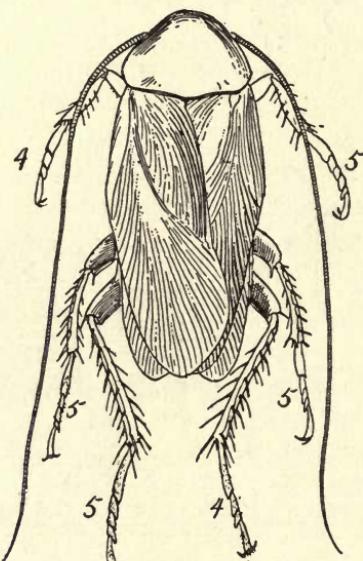


FIG. 60.

ialized a character as the color-pattern of the Lepidoptera, the evolutionary or species-forming factors find plenty of truly blastogenic variations in the group for working material.

Variation in Number of Tarsal Segments of *Periplaneta americana* (the American Cockroach).—A lot of 118 individuals (74 males, 39 females, 5 broken) of *Periplaneta americana*, the American cockroach, collected in December, 1894, in La Paz, Mexico, was examined for variation in the number of segments in the tarsi of the various feet (see fig. 60). Fourteen classes were found as follows:

Class A: 81 individuals (51 males, 26 females, and 4 so broken as to make it impossible to determine the sex) had all the feet 5-segmented.

Class B: 10 (8 males, 2 females) had the left hind foot 4-segmented.

Class C: 5 (2 males, 2 females, 1 broken) had right hind foot 4-segmented.

Class D: 5 (4 males, 1 female) had left middle foot 4-segmented.

Class E: 2 (1 male, 1 female) had right middle foot 4-segmented.

Class F: 4 (3 males, 1 female) had right fore foot 4-segmented.

Class G: 3 (2 males, 1 female) had left fore foot 4-segmented.

Class H: 2 (1 male, 1 female) had both hind feet 4-segmented.

Class I: 1 (female) had both middle feet 4-segmented.

Class J: 1 (male) had both fore feet 4-segmented.

Class K: 1 (male) had left hind foot and left fore foot 4-segmented.

Class L: 1 (female) had left hind foot and left middle foot 4-segmented.

Class M: 1 (female) had right hind foot and left fore foot 4-segmented.

Class N: 1 (female) had both hind feet and right middle foot 4-segmented.

Thus 71 per cent. had all the feet 5-segmented, which condition is one of the structural characteristics assigned by entomologists, not alone to this species or even genus of cockroaches, but to the whole cockroach family, the Blattidæ. The remaining 29 per cent. had one foot (29 cases), two feet (7 cases), or three feet (1 case) 4-segmented. Of the varying individuals 24 are males, 12 females, and five are so broken as to make the sex indeterminable, while of the normal individuals, 51 are males and 26 are females, a practically identical proportion, and considered in the light of the total numbers of males and females in the lot, a proportion indicating that the varying individuals are almost exactly evenly distributed between the two sexes.

Considering the conditions of correlation, right and left and segmental, it is obvious that the variations are influenced little by bilateral symmetry or metemerism.

Bateson, in his Materials for Variation (p. 415), records the finding by Brindley of 4-segmented feet (one or more) in 25 per cent. of a lot of adult individuals (number of individuals not given) of *Periplaneta americana*; in 15 per cent. of a lot of *Periplaneta orientalis*, and of *Blatta germanica*, 16 out of 102 individuals had one or more 4-segmented tarsi. Brisout de Barneville noted twenty years ago, or more, that a variation from five to four tarsal segments occurred occasionally in each of ten different species, representing four genera of cockroaches (Blattidae). Bateson records one specimen, species not given but evidently one of the three studied, as having all feet 4-segmented, and says that there was a slightly greater frequency in males than in females.

It being suggested to Bateson that, in view of the known power of regeneration of appendages, possessed by the Blattidae, these variations might be due to incomplete regeneration after mutilation, Bateson notes that in 200 just hatched individuals of *Periplaneta orientalis* no 4-jointed tarsus was found, "while in every instance of regeneration the new tarsus had four perfect joints," and concludes that "there can be no doubt that in the majority of cases, the 4-jointed tarsus had arisen on regeneration."

However, there is no difficulty in finding young roaches with 4-segmented feet. We have examined twenty immature individuals of *Periplaneta americana* belonging to the same collections lot as the adults referred to in the foregoing pages, and note the following conditions:

- Class A; 14 individuals (11 males, 1 female) had all the feet 5-segmented.
- " C; 2 individuals (males) had the right hind foot 4-segmented.
- " D; 2 individuals (males) had the left middle foot 4-segmented.
- " E; 1 individual (broken) had the right middle foot 4-segmented.
- " H; 1 individual (male) had both hind feet 4-segmented.

Thus 70 per cent. of the immature specimens examined had all feet 5-segmented and 30 per cent. showed variations. This is the same proportion as in the adults. The varying individuals, however, are 16 males to 1 female.

In another lot of individuals, 32 adults and 16 immature, of *Periplaneta americana* collected in Honolulu, 16 of the adults had all feet (not broken off) 5-segmented, while 16 had one or more 4-segmented feet; of the latter 5 have at least two 4-segmented feet. Of the immature individuals, 6 specimens had all the feet 5-segmented, while 10 had one or more feet 4-segmented.

In a mixed lot of *Periplaneta americana* and *Periplaneta australasiae*, 18 adult individuals have all the feet (not broken off) 5-segmented; 27 adult individuals have one or more feet 4-segmented (eight having two 4-segmented feet and 2 having three 4-segmented feet); 9 immature individuals have all the feet (not broken off) 5-segmented and 8 immature individuals have one or more feet 4-segmented (one having two 4-segmented feet and one having three 4-segmented feet).

In a series of 69 individuals of *Leucophea surinamensis* collected on the Island of Hawaii (Kohala Plantation) 54 adult individuals have all the feet (not broken off) 5-segmented; 8 adult individuals have one or more feet 4-segmented (two have two 4-segmented feet); 6 immature individuals have all the feet 5-segmented, while 1 immature individual has one 4-segmented foot.

But all these cases of 4-segmented feet are undoubtedly the result of natural regeneration after mutilation. At least¹ Brindley's elaborate experiments and exhaustive review of the observations of other men prove this nearly to moral certainty. He made hundreds of artificial mutilations of cockroach feet, and in all cases a 4-segmented tarsus was regenerated.

In the observations and experiments of Godelmann (Archiv f. Entw. mech. d. Org., 1901, Vol. XII, p. 265) on *Bacillus* (an orthopteron of the family Phasmidæ), it was shown that this insect, in regenerating legs, either after experimental amputa-

¹ Brindley, H. H., On certain characters of reproduced appendages in Arthropoda, particularly in the Blattidæ, Proc. Zool. Soc. Lon. 1898, pp. 924-958.

tion or voluntary self-mutilation by the throwing off of legs or parts of legs by the insects themselves, rarely regenerated five, the normal number of tarsal segments, but usually only three or four, thus creating a variation by regeneration.

It is interesting and puzzling to contemplate the curious conditions of these regenerative phenomena in Blattids and Phasmids. If having 5-segmented feet is an advantage to these insects (seized on and fixed by natural selection) and the capacity to regenerate feet after mutilation is an advantage, also fixed by natural selection, why should regenerated feet, as long, as strong, and apparently in every way as effective as 5-segmented feet, always be 4-segmented? This is a curious sort of regularly recurring discontinuous variation dependent on some stimulus connected with mutilation and regeneration.

Variation (Absent) in Number of Tarsal Segments of *Largus cincta*, *Anabrus simplex*, *Eleodes sp.*, and *Melanoplus femur-rubrum*.—A lot of 150 adult individuals of *Largus cinctus*, a sucking bug of the family Pyrrhocoridae, collected from two adjoining bushes of *Baccharis* on the campus of Stanford University, at one time, was examined for variation in number of tarsal segments. The insect has an incomplete metamorphosis. The normal tarsus is 3-segmented in all feet. No variation from this number was found.

A lot of 45 adult individuals (17 males, 28 females) of *Anabrus simplex* (western cricket), collected one day at Weiser, Idaho, was examined for variation in number of tarsal segments. The insect has an incomplete metamorphosis. The normal number of tarsal segments in all feet is four. No variation was found.

A lot of 123 adult individuals of *Eleodes sp.* (darkling ground beetle) collected at various times and localities in the vicinity of Stanford University was examined for variation in the number of tarsal segments. The insect has a complete metamorphosis. The normal number of tarsal segments is four in the hind feet and five in the fore and middle feet. No variation was found.

A lot of 105 adult individuals (60 females, 45 males) of *Melanoplus femur-rubrum*, the red-legged locust, collected at Ithaca, N. Y., in the summer of 1899, was examined for

variation in the number of tarsal segments. The locust has an incomplete metamorphosis. The normal number of tarsal segments, in all feet, is three, the first (basal) obviously being composed of the fused first three segments of a 5-segmented foot. Reversionary variation would be manifest in any increase in the number of segments, particularly, a breaking up of the first or basal compound segment into two or three distinct segments. In the 105 individuals (= 630 feet) examined no tarsus was found showing really any fewer or any more than three segments. In one female and in two males, one, or two, hind feet showed some constriction of the first (basal) segment, weakly indicating a subdivision into two parts.

Variation in Number of Tibial Spines of *Melanoplus femur-rubrum* (Red-legged Locust).—The locusts, or grass-hoppers, are insects with incomplete metamorphosis, the just-hatched



FIG. 61. The red-legged locust, *Melanoplus femur-rubrum*, and enlarged hind tibia showing inner (*i*) and outer (*o*) rows of spines.

young resembling in all important structural characters, except for the absence of wings, the adults. The larval and adult legs are identical structures. On the ventral (hinder aspect) of the tibiæ of the large posterior leaping legs are two rows or series of small but distinct spines, one along the outer edge, the other along the inner (fig. 61). The number of spines in this series has been used as a diagnostic character of the various species of the large genus *Melanoplus*.

A lot of 89 adult individuals (50 females, 39 males) of the red-legged locust, *Melanoplus femur-rubrum*, collected at Ithaca, N. Y., in a brief time period, was examined to determine

the variation in number of the tibial spines on the hind legs. The range and frequency of this variation is shown in the following frequency polygons:

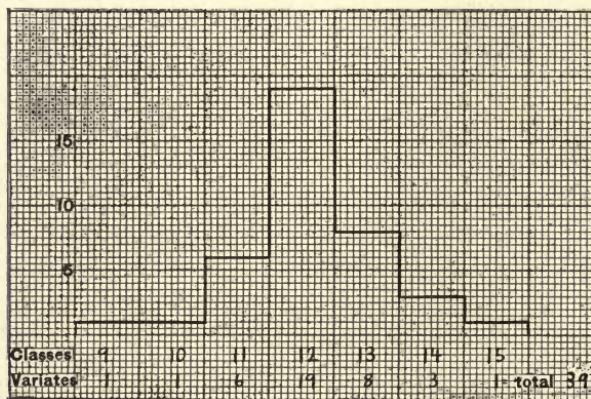


FIG. 62. Frequency polygon of the variation in number of spines in the outer row of the right tibiae in 39 male red-legged locusts, *Melanoplus femur-rubrum*.

From these polygons it will be noted that the range is, in outer row, right tibia, males, 9 to 15, females 11 to 15; left

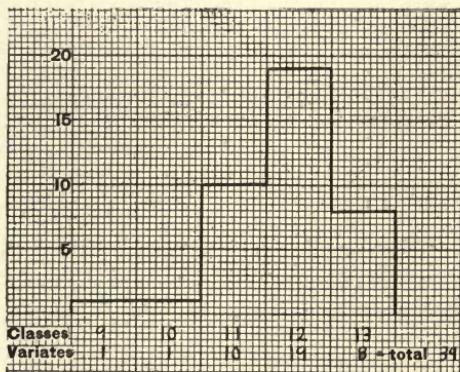


FIG. 63. Frequency polygon of the variation in number of spines of the outer row on left tibiae of 39 male red-legged locusts, *Melanoplus femur-rubrum*.

tibia, males, 9 to 13, females 10 to 14; in inner row, right tibia, males, 11 to 14, females 10 to 14, left tibia, males, 11 to 14,

females 12 to 16. The mode for the outer row in both males and females is 12, for the inner row 12, with 13 nearly as frequent. Although the series are too short to afford fair con-

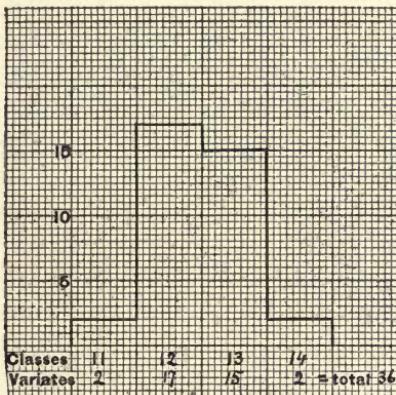


FIG. 64. Frequency polygon of the variation in number of spines in the inner row on right tibiae of 36 male red-legged locusts *Melanoplus femur-rubrum*.

clusions from statistics, it is obvious that the frequency and range of the numbers of spines above the mode are larger than

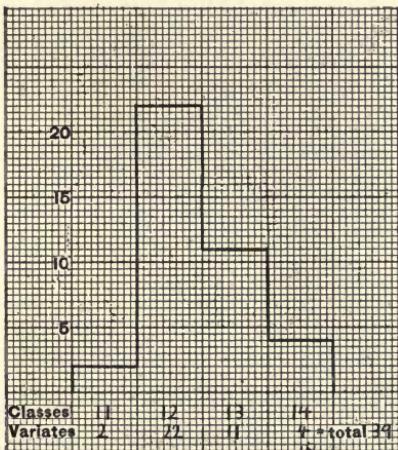


FIG. 65. Frequency polygon of the variation in number of spines in inner row of left tibiae of 39 male red-legged locusts, *Melanoplus femur-rubrum*.

those below the mode, indicating the course of evolutionary movement.

In Scudder's Monograph of the Melanoplinae (1899) 129 species of *Melanoplus* are described, for 127 of which the number of tibial spines in the outer row is used as a specific character, certain variation within definite limits being ascribed to most

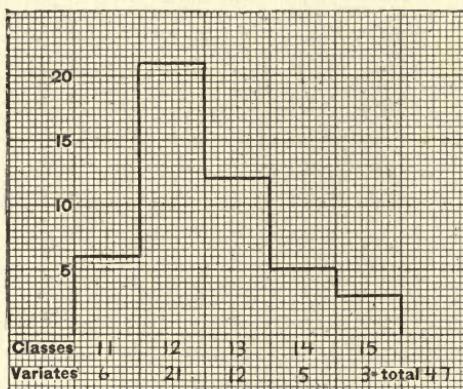


FIG. 66. Frequency polygon of the variation in number of spines in outer row of right tibiae of 47 female red-legged locusts, *Melanoplus femur-rubrum*.

of the species. The number ascribed to *femur-rubrum* is "10 to 13, usually 11." The range, in males alone, of our short series covers all the typical numbers of spines (outer row) recorded and

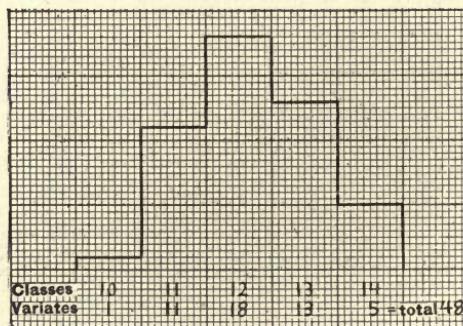


FIG. 67. Frequency polygon of the variation in number of spines in outer row of left tibiae of 48 female red-legged locusts, *Melanoplus femur-rubrum*.

used diagnostically for all the species in Scudder's Monograph.

There are no discernible marked differences between males and females in the extent and character of the variations.

Looking to the correlation of the number of spines in outer and inner row of same leg, in outer rows of right and left legs of same individual, and in inner rows of right and left legs of same individual the following conditions obtain in our series :

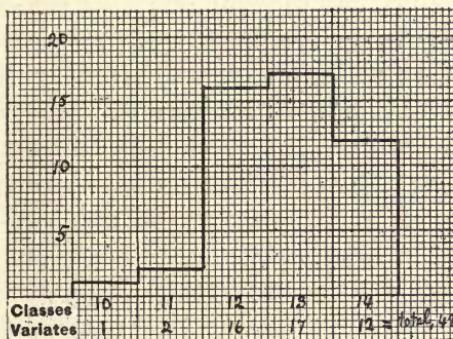


FIG. 68. Frequency polygon of the variation in number of spines in inner row of right tibiae of 48 female red-legged locusts, *Melanoplus femur-rubrum*.

In outer and inner rows of right tibiae : in males (39) numbers were the same in 15 cases, numbers differed by one in 19 cases, numbers differed by two in 3 cases, numbers differed by three in 2 cases ; in females (50) numbers were the same in 17 cases,

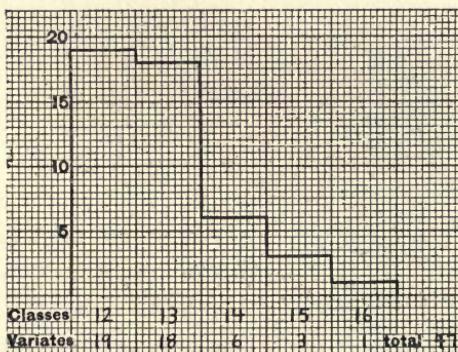


FIG. 69. Frequency polygon of the variation in number of spines in inner row of left tibiae of 47 female red-legged locusts, *Melanoplus femur-rubrum*.

numbers differed by one in 22 cases, numbers differed by two in 8 cases, numbers differed by three in 2 cases.

In outer and inner rows of left tibiae : in males (39) numbers were the same in 19 cases, numbers differed by one in 13 cases,

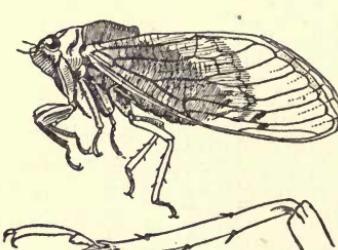
numbers differed by two in 6 cases, numbers differed by three in 1 case; in females (50) numbers were the same in 15 cases, numbers differed by one in 24 cases, numbers differed by two in 9 cases, numbers differed by three in 1 case.

In corresponding rows in right and left tibiæ. In outer rows of males (39) numbers were the same in 17 cases, numbers differed by one in 15 cases, numbers differed by two in 5 cases, numbers differed by three in 2 cases; of females (50) numbers were the same in 25 cases, numbers differed by one in 16 cases, numbers differed by two in 7 cases, numbers differed by three in 1 case. In inner rows: of males (39) numbers were the same in 20 cases, numbers differed by one in 18 cases, numbers differed by two in 1 case, numbers differed by three in no case; of females (50) numbers were the same in 16 cases, numbers differed by one in 24 cases, numbers differed by two in 8 cases, numbers differed by three in 1 case.

This case of variation, as well as numerous others in our list, notably that of the antennal segments of *Phenacoccus* (p. 311), which have to do with characters that happen to be ones used by systematists in classification, illustrates what an informing light statistical studies of variation have to throw upon systematic practise.

The modern *systematist* will have to take into account the actual status of the existent variation in the characters of which diagnostic use is made.

Variation in Tibial Spines of Cicada septendecim (the Seventeen-year Locust or Periodical Cicada).—The periodical cicada



(family Cicadidae, order Hemiptera) has an incomplete metamorphosis, the young or larval stage being passed underground in active burrowing about and feeding. The fore legs are fitted for digging but the middle and hind legs are purely locomotory. On the ventral aspect of each hind tibia there are certain small but distinct spurs or spines arranged in two longitudinal series, one along the outer margin of this aspect, the other along the inner (fig. 70).

FIG. 70.

The variation in number of the setibial spines was determined in a lot of 150 individuals (100 males, 50 females), collected by B. T. Riley at Indianapolis, Indiana, in the summer of 1898. The following frequency polygons show the character of this meristic variation.

As will be seen from the frequency polygons the range in the

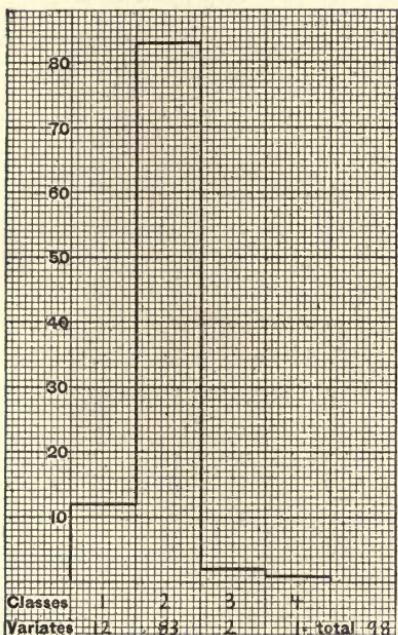


FIG. 71. Frequency polygon of the variation in number of spines in outer row of right tibiæ of 98 male seventeen-year cicadas, *Cicada septendecim*; mean, 1.9; index of variability, .42; coefficient of variation, 2.21.

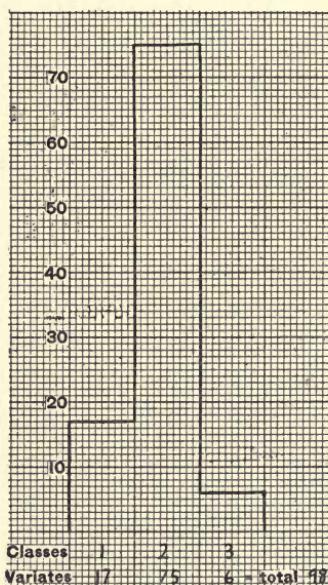


FIG. 72. Frequency polygon of the variation in number of spines in outer row of left tibiæ of 98 male seventeen-year cicadas, *Cicada septendecim*; mean, 1.9; index of variability, .47; coefficient of variation, 2.47.

outer row of right tibiæ in males (100 specimens), is 1 to 4, left tibiæ 1 to 3; right tibiæ of females (50 specimens), 1 to 3, left tibiæ 1 to 3; in inner row of right tibiæ in males, 1 to 5, left tibiæ 2 to 5; right tibiæ of females, 2 to 5, left tibiæ, 2 to 5. The mode in outer rows is 2, the inner rows 3 and 4 are nearly equal modes. In the outer rows it will be noted that the num-

ber (1) below the mode (2) is more abundantly represented than the numbers (3 and 4) above the mode. In the inner rows the curve of frequency is nearly perfectly symmetrical, with a very high modal point, and nearly equal in extent and character on each side of this point.

To indicate the degree of correlation of the variation in number of spines in the various individuals of this series studied, the following compilation has been made:

Taking the number of spines in the inner rows of the right and left tibiæ of the same individual there are, among the

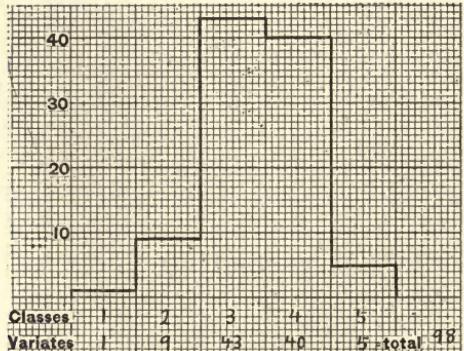


FIG. 73. Frequency polygon of the variation in number of spines in inner row of right tibiæ of 98 male seventeen-year cicadas, *Cicada septendecim*; mean, 3.4; index of variability, .66; coefficient of variation, 19.4.

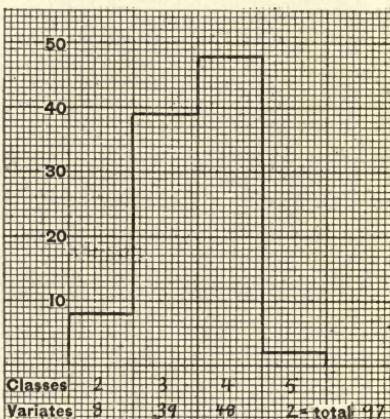


FIG. 74. Frequency polygon of the variation in number of spines in inner row of left tibiæ of 97 male seventeen-year cicadas, *Cicada septendecim*; mean, 3.25; index of variability, .7; coefficient of variation, 21.5.

males (only 50 individuals taken at random from the series of 100, in order to make the comparison with the 50 females more obvious): 39 individuals with combinations of 3-3, 3-4, or 4-4 spines (both modes); 7 individuals with combinations of 3-2 spines (mode and below); 2 individuals with combinations of 2-2 spines (both below mode); 1 individual with combination of 5-3 spines (above mode and below); 1 individual with combination of 1-4 spines (extreme difference).

Among the females there are: 42 individuals with combina-

tions of 3-3, or 4-4 spines (both modal); 3 individuals with combinations of 3-2 spines (mode and below); 3 individuals with combination of 4-5 spines (mode and above); 1 individual with combination of 4-2 spines (extreme difference).

In the outer rows of right and left tibiae of the same individual there are, among the males (same 50): 31 individuals with

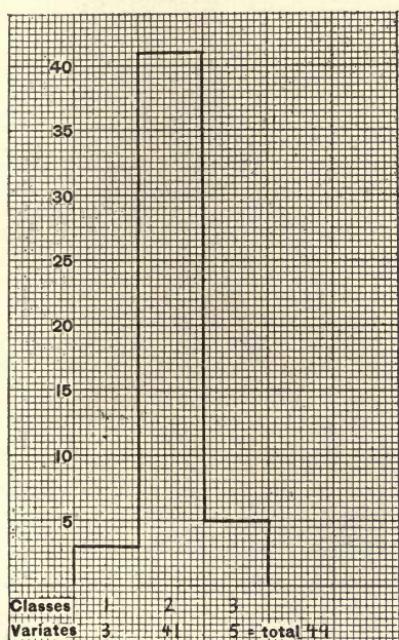


FIG. 75. Frequency polygon of the variation in number of spines in outer row of right tibiae of 49 female seventeen-year cicadas, *Cicada septendecim*; mean, 2; index of variability, .04; coefficient of variation 2.

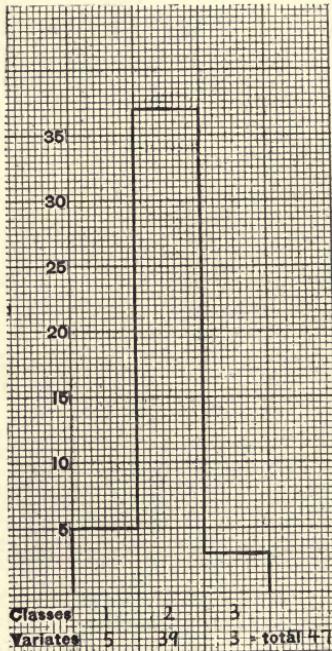


FIG. 76. Frequency polygon of the variation in number of spines in outer row of left tibiae of 47 female seventeen-year cicadas, *Cicada septendecim*; mean, 2.; index of variability, .04; coefficient of variation 2.

combinations of 2-2 spines (both modal); 15 individuals with combinations of 1-2 spines (mode and below); 4 individuals with combinations of 2-3 spines (mode and above).

Among the females there are: 44 individuals with combinations of 2-2 spines (both modal); 8 individuals with combinations of 1-2 spines (mode and below); 6 individuals with combinations of 2-3 spines (mode and above).

Variation in Actual and Relative Length of Segments of the Antennæ of *Ceroputo yuccæ* (?) (a Scale Insect).—In the systematic study of the Coccidæ (scale insects) the actual and relative length of the various segments composing the antennæ are often used as specific characters. The Coccidæ are insects with incomplete metamorphosis, and the larval and adult antennæ are identical structures showing however some developmental change; in many Coccidæ there is one segment fewer in

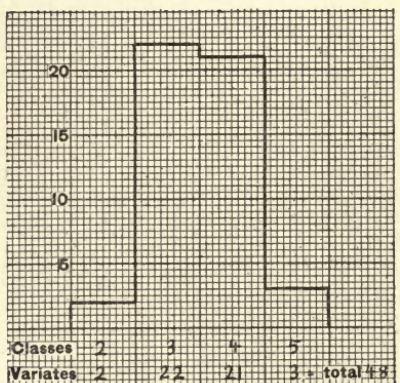


FIG. 77. Frequency polygon of the variation in number of spines in inner row of right tibiae of 48 female seventeen-year cicadas, *Cicada septendecim*; mean, 3.52; index of variability, .67; coefficient of variation 19.3.

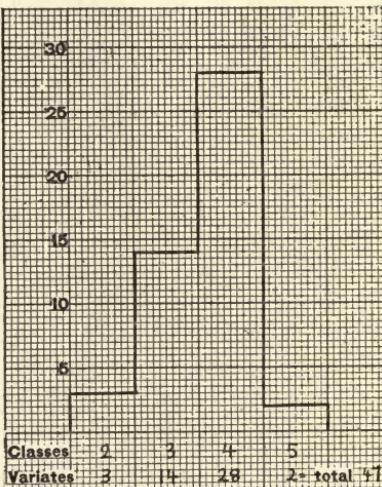


FIG. 78. Frequency polygon of the variation in number of spines in inner row of left tibiae of 47 female seventeen-year cicadas, *Cicada septendecim*; mean, 3.62; index of variability, .67; coefficient of variation 18.5.

the antennæ during larval life. The relative lengths are indicated by a formula composed of the ordinal numbers of the segments (segment one being the basal one) (fig. 79) arranged in linear series beginning with the number of the longest segment followed by the number of the next to longest and so on. There are at present known six North American species of *Ceroputo* and 34 species of *Phenacoccus*, a closely allied genus, to which most of the *Ceroputo* species were first ascribed, and in the specific diagnoses of nearly all, the "antennal formula" is

used as a diagnostic character, as shown in the following examples:

Phenacoccus pergandei Ckll. (*Psyche*, 1896, supp., p. 19).
Formula: 3, 2,¹ (1, 4, 5, 6, 9), (7, 8).

P. gossypi Ckll. (*Jour. N. Y. Ent. Soc.*, 1898, Vol. VI, p. 170). Formula: 2, (3, 9), (1, 4, 5, 6, 7, 8).

P. artemesiæ Ehr. (*Canad. Ent.*, 1900, Vol. XXXII, p. 313).
Formula: 2, 3, 9, 1, 4, (5, 6, 7, 8).

P. stachyos Ehr. (*Canad. Ent.*, 1900, Vol. XXXII, p. 314).
Formula: 3, 2, (4, 5), 9, (1, 6), 7, 8.

P. minimus Tins. (*Canad. Ent.*, 1898, Vol. XXX, p. 223).
Formula: 9, (2, 3) 1, 6, 7, (4, 5, 8).

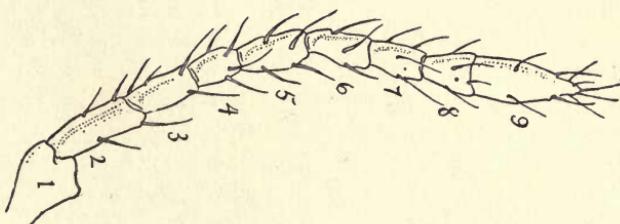


FIG. 79. Antenna (greatly enlarged) of the scale insect, *Ceroputo yuccæ*, with segments numbered.

P. solenopsis Tins. (*Canad. Ent.*, 1898, Vol. XXX, p. 47).
Formula: 2, 9, 3, (1, 5) 4, (6, 7) 8.

P. americæ Ckll. (*Canad. Ent.*, 1897, Vol. XXIX, p. 91).
Formula: 9, 1, 3, 2, (8, 7), (4, 5, 6).

P. simplex King. (*Ent. News*, 1902, Vol. XIII, p. 42).
Formula: (3, 9), (1, 2), 8, 6, (5, 7), 4.

P. wilmattæ Ckll. (*Ann. and Mag. Nat. Hist.*, 1901, ser. 7, Vol. VIII, p. 57). Formula: 2, 9, 3, 1, 5, (4, 6, 7, 8).

Ceroputo yuccæ barberi Ckll. (*Bull. 4, Tech. Series, Div. Ent. U. S. Dept. Agric.*, p. 39). Formula: 9, 3, (1, 2, 4, 5, 6, 7,) 8.

C. bahiæ Ehr. (*Canad. Ent.*, 1900, Vol. XXXII, p. 314).
Formula: 3, 5, 9, 6, 7, 4, 8, 1, 2.

In the examination of the antennæ of twenty-five female individuals of *Ceroputo* (*Phenacoccus*) *yuccæ* (?) (if not *yuccæ*

¹ Segments in parenthesis are of equal length.

this is a new species) the following conditions with regard to the variation in actual and relative lengths of the antennal segments was noted: writing out the formula for each antenna in the series (a total of 50, two antennæ on each individual), based on careful measurements with micrometer, and comparing these formulæ, it was found that no two formulæ agree, and that there was practically as much variety in these formulæ as there is among the eleven formulæ published as specifically diagnostic for eleven North American species of the genera *Ceroputo* and *Phenacoccus*.

The formulæ for the 50 antennæ of the 25 individuals are as follows:

1. L. broken.
R. 9, 3, 2, (1, 8), (6, 7), (4, 5).
2. L. broken.
R. 9, 3, 2, 1, (4, 8), (5, 6, 7).
3. L. 9, 3, 2, (1, 5, 8), 4, (6, 7).
R. 9, 3, (1, 2), 8, (4, 5, 6, 7).
4. L. (8, 3), (1, 2, 7), (4, 5, 6).
R. (8, 3), 2, (1, 7), 6, (4, 5).
5. L. 9, 3, 2, 1, (5, 6, 7, 8), 4.
R. 3, 9, 2, 1, (7, 8), 5, 4, 6.
6. L. (9, 3), (1, 2), 8, (4, 5, 6, 7).
R. 3, 9, 2, (1, 5, 8), 4, 6, 7.
7. L. 9, 3, 2, 1, (4, 7, 8), (5, 6).
R. 9, 3, 2, 1, 4, (5, 6, 7, 8).
8. L. broken.
R. (9, 3), (1, 2), 8, (4, 5, 6, 7).
9. L. broken.
R. (8, 3), 1, 5, 2, (4, 7).
10. L. 3, 9, (1, 2), 5, (4, 7, 8), 6.
R. 8, 3, 4, (1, 2), 7, (5, 6).
11. L. (9, 3), (1, 2), (7, 8), (4, 5, 6).
R. 9, 3, 2, 5, 8, (4, 5, 6, 7).
12. L. 9, 3, (1, 2), 8, 7, (4, 5, 6).
R. 9, 3, 1, (2, 8), (5, 7), (4, 6).
13. L. 8, 3, (2, 4), 1, (6, 7), 5.
R. (8, 3), 4, 2, 7, (1, 5, 6).
14. L. (9, 3), (1, 2), 8, 7, 5, 6, 4.
R. 9, 3, (1, 2), (5, 4, 8), (6, 7).
15. L. (9, 3), 2, 1, 8, 7, 6, 5, 4.
R. 9, 3, 2, (1, 7, 8), (4, 5, 6).
16. L. 9, 3, 2, (5, 8), 6, (4, 7).
R. 9, 3, (1, 2, 8), (4, 5, 6, 7).
17. L. broken.
R. (9, 3), 2, (1, 8), (4, 5, 7).
18. L. broken.
R. broken.
19. L. (9, 3), 2, 1, 8, 4, 7, (6, 8).
1 R. broken.
20. L. 9, 3, 2, 1, (7, 8), (4, 5, 6).
R. 3, 9, 2, 1, 8, 7, (4, 6), 5.
21. L. 9, 3, 2, 8, (1, 4, 5, 7), 6.
R. 9, 3, 2, (5, 1, 8), (4, 7), 6.
22. L. 3, 8, 1, 4, 2, 7, (5, 6).
R. 3, 8, 4, (1, 2), (5, 6, 7).
23. L. 9, 3, 6, (1, 7, 8), 6, (4, 5).
R. 9, 3, 2, 1, (6, 7, 8), (4, 5).
24. L. broken.
R. broken.
25. L. 3, 9, (1, 2), (4, 5, 6, 7, 8).
R. 9, (2, 3), 1, (4, 5, 8), 7, 6.

In actual lengths the antennal segments varied as follows, (only the range given): Seg. 1, 4-7; seg. 2, 4-8; seg. 3, 6-11; seg. 4, 3-8; seg. 5, 3-5; seg. 6, 3-4½; seg. 7, 3-5½; seg.

8, 4-9; seg. 9, 7-9. The length numbers refer to units of the micrometer scale, not reduced to millimeter fractions.

It is surely obvious, as has been mentioned before in connection with the account of the variations in the number of tibial spines of *Melanoplus femur-rubrum* (p. 34) that systematic students of zoölogy must take into account the conditions of variation exhibited by the characters they choose for use in specific diagnoses. Students of variation may never supply biology with "a precise criterion of species" but they can very promptly supply the systematist with a precise criterion of the stable value of any specific character.

Variation (Absent) in Number of Antennal Segments in *Eleodes* sp. and *Vespa* sp.—In a lot of 123 adult individuals of *Eleodes* sp., a darkling ground beetle, collected at various times and places near Stanford University, no variation in the number of segments composing the antennæ was found. The normal number is eleven. The insect has a complete metamorphosis.

In a lot of 55 adult individuals of *Vespa* sp., yellow-jacket, collected on one day in one place (feeding on refuse), on the Stanford University campus, no variation in the number of segments composing the antennæ was found. The normal number of antennal segments is thirteen. The insect has a complete metamorphosis. The same individuals show considerable variation in pattern of abdominal markings (see p. 284).

Variation in Number of Long Tactile Hairs on the Metathorax of *Lipeurus celer* and *L. varius* (Biting Bird Lice).—The biting bird lice, or Mallophaga, are external wingless parasites on birds and mammals, living their whole life on the body of their host or in some cases on the bodies of two or more hosts, migrating from parent to young in nesting time, from one sex to another in mating time, or from one companion to another in the case of crowding, gregarious species. Their migrations however, are practically limited to passing directly from one host to another when the hosts are in actual contact and the majority of parasitic individuals undoubtedly spend the whole life from egg to death on one host. Thus there exists a pronounced isolation of groups of individuals on individual hosts

and necessarily much in-and-in breeding. It is a condition analogous to island life carried to an extreme of isolation of small groups of individuals of the same species. The metamorphosis of the Mallophaga is incomplete.

On the latero-posterior angles of the dorsum of the metathorax of all species of the genus *Lipeurus*, parasitic on birds, are certain very long, spine-like hairs (fig. 80), probably tactile in function, whose number and arrangement vary in different species, but are presumably constant for any given species. The number of these hairs is used to some extent in distinguishing-

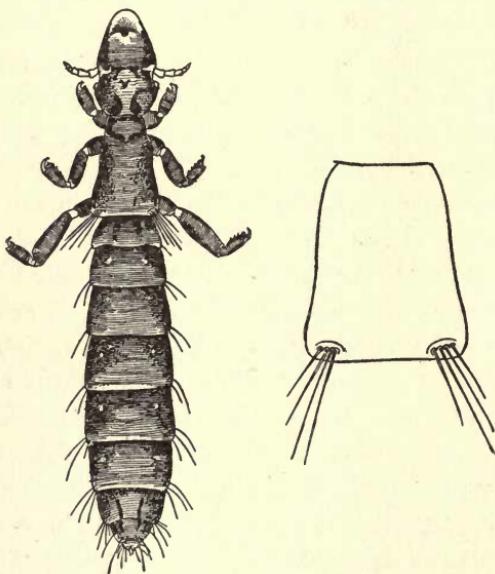


FIG. 80. The biting bird louse, *Lipeurus celer*, and diagram of metathorax (enlarged) showing tactile hairs in lateral posterior angles.

ing species of the genus. We have examined the variation in number of these hairs in 239 individuals of *Lipeurus celer* Kell., a parasite of the fulmars, *Fulmarus glacialis* vars. *rodgersi* and *glupischka*. These individuals were taken from 31 *Fulmarus glacialis* hosts, shot in the Bay of Monterey, California, in a time period of two weeks.

The range in number of the tactile hairs is from 3 to 6, with 4 as the mode, the mode occurring in a large majority of cases.

Out of the 239 individuals the hairs could be accurately determined on the right side in 189 cases, on the left in 193, the frequencies being as follows:

On the right side: 2 individuals have 3 hairs, 177 individuals have 4 hairs, 10 individuals have 5 hairs.

On the left side: 3 individuals have 3 hairs, 185 individuals have 4 hairs, 4 individuals have 5 hairs, 1 individual has 6 hairs.

The mean on the right side is 4.04, on the left side 4.01; the standard deviation on right side .248, on left side .238; the coefficient of variation on right side is 6.15, on left side 5.92.

The few cases of variation from the mode, 4 hairs, were scattered in various groups of individuals, letting all the parasites from an individual host constitute a group. That is, the variation was not associated with isolation. From one host were taken ten parasites of which one had 5 hairs on one side, one 3 hairs on one side and all the others 4 on each side; from another host were taken twenty-six parasites, the number of hairs on each side of all the individuals being 4 except one case of 5 on one side, and so on. The twenty cases of variation from the mode were distributed in ten groups of parasites, *i. e.*, occurred in parasites from ten out of the thirty-one host individuals.

The correlation conditions (degree of bilateral symmetry) of the variations are shown by the following summary (only 183 specimens out of the 239 had the hairs so intact that the exact number of hairs on both sides of the metathorax could be determined):

Of 183 individuals, 166 have 4 hairs (the mode) on each side, the remaining having hairs as follows: nine have 4 on one side and 5 on the other, five have 4 on one side and 3 on the other, two have 5 on each side, one has 4 on one side and 6 on the other, none has the combination of 3 and 5.

In 72 specimens of *Lipeurus varius* taken from 29 specimens of *Fulmarus glacialis* vars. *rodgersi* and *glupischka* (Bay of Monterey, time period, two weeks), the range of variation in number of metathoracic tactile hairs is 3-5 with 4 as a very dominant mode, the frequencies being as follows:

On the right side: 13 individuals have 3 hairs, 49 individuals have 4 hairs, 2 individuals have 5 hairs.

On the left side: 14 individuals have 3 hairs, 48 individuals have 4 hairs, 2 individuals have 5 hairs.

The mean on right side is 3.83, on left side 3.81; the standard deviation on right side .453, on left side .463; the coefficient of variation on right side is 11.98, on left side 12.16.

From these figures it is seen that in this species of *Lipeurus* the variates possessing three hairs greatly outnumber the variates possessing five hairs. This might be interpreted to mean that the species is tending toward a form possessing three tactile hairs instead of four, or alternately that the present form with four hairs is developing (evolving) from an older form with three. The coefficients of variation for this character are much larger (twice as large) in this species than in *L. celer*.

Examining the distribution of the variations by isolated groups of individuals (each group from a single bird host) the thirty-one variations are distributed among eleven groups out of the total twenty-nine groups. In no group in which there was a case of the occurrence of 5 hairs, was there an occurrence of 3 hairs (the largest group in which 5 hairs occurred contains only five individuals). In a group of twelve individuals three have 3 hairs on each side, and a fourth has 3 hairs on one side and 4 on the other, while the remaining eight have 4 hairs on each side; in a group of ten individuals three have 3 hairs on each side, a fourth has 3 hairs on one side and 4 on the other, while the others have 4 hairs on each side.

With regard to correlation between right and left side, forty-four individuals of sixty two (in which the hairs on both sides could be accurately determined) have 4 hairs on each side; twelve have 3 on each side, two have 4 on one side and 5 on the other, and one has 5 on each side.

Variation in the Character of the Elytral Striae of *Pterostichus* sp. (Predaceous Ground Beetle).—The ground beetles of the genus *Pterostichus* have about ten fine longitudinal grooves on each elytron (Fig. 81). These grooves present manifold variation in their make-up, any one appearing as a continuous line, as a broken line, as a forking or branching line, or coa-

lescing with its left or right-hand neighbor. In a lot of 149 individuals collected under stones on a hillside near San Jose, on April 4, 1903, a number of classes were established on the basis of the character of the two lines, one on each elytron, lying on either side of the median groove which indicates the suture of fusion of the inner margins of the two elytra. These lines are referred to as α^l and α^r and either may have a short branch called α^{lb} or α^{rb} , or simply α^b when referred to for both sides (fig. 81.)

The beetles are insects of complete metamorphosis and their imaginal structural characters appear at once, on the issuance

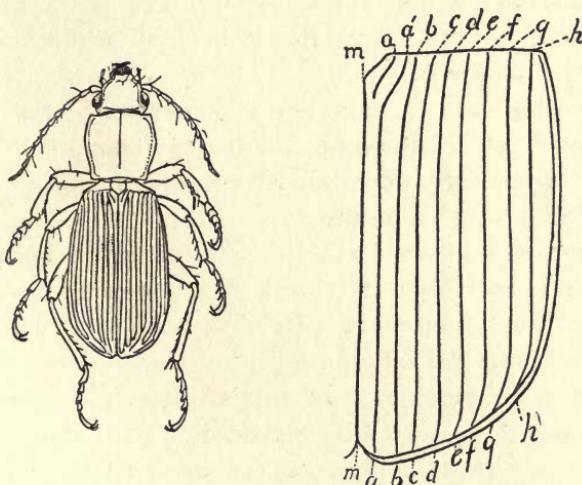


FIG. 81. The predaceous ground beetle, *Pterostichus* sp., and diagram of elytron (much enlarged), showing striae.

of the imago (after the brief necessary expanding and drying of wings, appendages and body-wall) in definite and fixed condition. Variations in these elytral striae are to be looked on as strictly congenital in character.

The classes and their frequencies based on the variations in the character of lines α^l and α^r in the lot of 149 individuals are as follows:

Class A: 102 individuals have lines α^l and α^r separate on both elytra.

Class B: 4 individuals have line α^b continued to line α on both elytra.

Class C: 5 individuals have line α broken off and α^b continued on both elytra.

Class D: 4 individuals have line α^b separate and line α broken, then continued below on both elytra.

Class E: 6 individuals have line α^{rb} continued to line α^r and line α^b separate.

Class F: 8 individuals have line α^b continued to line α^l and line α^r separate.

Class G: 7 individuals have line α^{rb} separate, line α^b separate and line α^l broken, then continued below.

Class H: 2 individuals have line α^{rb} separate, line α^r broken, then continued below and line α^b separate.

Class I: 3 individuals have line α^r broken, and α^{rb} continued below, line α^b separate.

Class J: 3 individuals have line α^{rb} separate, line α^r broken, then continued below, line α^b continued to line α^l .

Class K: 1 individual has line α^{rb} continued and a cross line between α^{rb} and α^r , α^b separate.

Class L: 2 individuals have line α^b separate in both elytra.

Class M: 1 individual has line α^{rb} separate at first, line α^r broken, then continued below, its end connected with a line below line α^{rb} , and line α^b separate.

Class N: 2 individuals have line α^{rb} separate, line α^b continued below and connected by a cross line with α^l .

In the above series the classes have been established on the basis of one pair of lines or grooves. An attempt was made to separate the lot of individuals into classes based on the variation manifest in all the lines, with the result that *no two individuals* could be put into the same class. The variation in these lines apparently exhausts the possibilities of combinations of various conditions in the members of the line series. That these minute, although to the trained and microscope-aided eye distinct, variations can be of life and death selective pattern-value (and any other function for these lines than the making of pattern is not apparent) seems inconceivable. But in numerous cases the presence or absence, and even the arrangement and character of these fine elytral striæ are characteristics diagnostically used by systematists in their keys to genera of

beetles of the family Carabidæ (to which family *Pterostichus* belongs). In the family Dytiscidæ (predaceous water-beetles) the elytral striæ are also used as classificatory characters. A curious female dimorphism exists in some Dytiscid species in which one form of female has the elytra deeply grooved, while the other form has smooth elytra. The significance of this dimorphism is not known.

GENERAL RESULTS AND SIGNIFICANCE.

Blastogenic and Acquired Variations. — The importance of distinguishing, in any study of variation considered as a factor in species-forming, between those variations in the animals under observation which are truly blastogenic and those which are, in part at least, acquired by reaction to some causative influence from without during the immature life (development) of the individuals is obvious. If acquired characters are non-heritable, then, while the rigor of selection among adults may and will take into account any variations, either blastogenic or acquired which may exist in these adults, the selected survivors will, in fact, tend to transmit, and thus retain in the species, only those variations which are blastogenic. If acquired characters are heritable then the importance, perhaps, although not the interest of such a distinction between the two categories of variation may be lessened. But undoubtedly a majority of working naturalists believe that the inheritance of acquired characters is yet unproved.

With the importance of this distinction well in mind — indeed with the belief that variation study without this distinction in mind has not much claim to attention from biologists intent on discerning the factors in a method of evolution — we have tried to point out in this paper in the case of each insect or characteristic studied, the character, blastogenic or acquired, which the variations discussed possess. For example, the variations in the pattern of *Diabrotica*,¹ *Hippodamia* and *Vespa* (insects of complete matamorphosis with all adult external structures

¹ By reference to the table of contents the position in this paper of the particular discussion of any variation referred to in this general part of the paper may be found.

never exposed in definitive unchangeable condition to outside influences) are blastogenic variations, as are also the structural variations in the character of the venation and the number of costal hooks in *Apis* and in the black ant that was studied but the variations in the pattern of the pronotum of *Tettigonia*, *Corisa*, the capsid and flower bug, and the number of tibial spines in *Cicada* and *Melanoplus*, may be in part acquired, for in these latter cases the insects are exposed during their immature life (development), with these color and structural characters in formative condition, and to some extent in use, to the continuous influence of their environment.

Given a criterion (either in the character of the variation, or the variable character itself, or in the life history of the animal showing the variations) that will enable one to distinguish between strictly blastogenic variations and those which may be wholly or in part acquired—and we believe we have such an one and a particularly valid one, in the case of the insects with complete metamorphosis—and this criterion may be applied not only to an individual but to an hereditary series of individuals and the larger question—that *Streiffrage* of modern biology—as to the transmission of acquired variations be approached through breeding. By comparison of series of generations whose immature life has been exposed to various (experimentally controlled and quantitatively determined) conditions of life, with series of generations whose immature life is exposed to only a single rigidly controlled set of life conditions may be determined not only the effect of varying conditions on the production of variations, but the heritability of these variations. The most satisfactory answer to the question of the hereditary transmission of acquired characters will come as the result of a quantitative (statistical) study of variations known to be blastogenic compared with a similar study of variations known to be acquired, both studies to be made on complete series of individuals bred under quantitatively determined life conditions. Such studies are certainly not impossible, with a criterion for the distinction between blastogenic and acquired variation once obtained. The character of this criterion, for insects, exists by reason of the effective difference in the course of the life his-

tory as regards insects of complete metamorphosis, and has been already explained in the introduction.

Continuous and Discontinuous Variation.—By continuous variations we mean to refer to those variations variously called fluctuating, individual, etc., which are present in any series of individuals of a species, and which cluster about the modal or most abundantly represented form of the species as would be expected from the law of error (law of probabilities). Although the extremes (at either end of the range) among these variations may differ considerably, they are so connected with the mode, by such a nearly perfect series of gradatory or intermediate steps, that a curve or polygon graphically expressing their frequency and range will usually (where the number of individuals in the series examined is large enough to exhibit the actual conditions of variation in the species) correspond closely to the theoretical curve which may be plotted for the species on the basis of the law of error. Although Morgan (*Evolution and Adaptation*) objects to the use of "continuous" as a descriptive name for these variations, on the ground that the word suggests persistence or continuity through successive generations, it seems to us that the name is apt if "continuous" be taken to mean that the occurring variations in any (sufficiently large) set of individuals form a continuous series, the extremes being connected or immediately merging into each other by a series of small gradatory steps. By discontinuous variations we would mean, in contrast to continuous, such considerable and radical variations as have been variously called single variations, sports, mutations, etc., that is, variations, which are not members of a gradatory series, do not group themselves in orderly manner about the modal species form according to the law of error, and although often not large are yet rarely so minute as those differences which distinguish the adjacent members in any series of individuals arranged on a basis of continuous or fluctuating variation. Mutations, according to the usage of De Vries, our discontinuous variations may or may not be. Thus, all mutations might be called discontinuous variations, although not all discontinuous variations are necessarily De Vriesian mutations, that is, certain to breed true under varying conditions of environment.

As a matter of fact not all continuous variation follows the law of error; the curve or polygon of frequency is not infrequently an asymmetrical one; "skewness" prevails, or the curve may even be bi-modal. But nevertheless the "continuity" of the variations is unmistakable. In a sufficiently large series the extremes of the range are perfectly connected with the mode or modes and hence with each other by gradatory steps very small in size. Whatever the largeness of the difference between the extremes, any two adjacent members of the series are hardly distinguishable. This gradual, insensible but yet effective (as regards widely separated members of the series) kind of variation is most typically illustrated in cases of what Bateson calls "substantive" variation, that is, where the varying characteristic is one of pattern, of length, width, or bulk, of the curving of a vein or leg or spine. Excellent examples of this continuous substantive variation are presented by the abdominal and face patterns of *Vespa* (see p. 284), the elytral pattern of *Diabrotica* (see p. 274), the prothoracic pattern of *Corisa* (see p. 293) and others. According to Bateson, variations in number of antennal and tarsal segments, number of spines, hairs or other processes, and often such numerical or, as called by him, meristic variations, must be looked on as different in kind from the substantive variations;—those capable of perfect emergence from one condition to another, in other words, practically incapable of quantitative measurement. These meristic variations are called discontinuous by Bateson. Numerous typical examples are included in our data. (See the accounts of the variation of the number of the costal wing-hooks in bees and ants, the number of tibial spines in the locust and the cicada, the number of metathoracic tactile hairs in biting bird-lice, etc.) But when one stops to consider the fact that in all these cases variation could hardly occur by any less steps than those of one hook or one spine or one hair, that a half hook or half antennal segment is inconceivable, some serious doubts as to the validity of Bateson's classification of variations as continuous and discontinuous will certainly result. The doubt is strengthened by the difficulty of a clean classification presented by such cases as that of *Hippodamia convergens*. Here we have a substantive

variation in pattern, appearing, however, in such a way as to demand numerical, *i. e.*, meristic, expression. One specimen has 9 elytral spots, another 10, another 11, and so on; the whole range is indeed from 0 to 18, with every number between represented, each by various combinations of spots. But it is conceivable, and indeed is really the case among our specimens, that these spots might be either of normal size, or of any lesser size down to the limits of visibility. Some of the spots are of the diameter of pin-points; some of the pin-shaft and some pin-heads. There is perfect gradation or continuity in this variation. But even in such cases as variations in spines and hairs, this gradation might exist; and indeed does. Although in our consideration of the variation in the number of the tibial spines of the locust and the cicada and in the number of the tactile hairs of the bird-lice, we have referred to these variations only numerically, *i. e.*, meristically, as a matter of fact there are obvious differences in the length, *i. e.*, size, of the spines and hairs, so that it would be wholly fair to break down the unit differences and speak of differences by one-quarter, one-third and two-thirds of a spine. For the tibial spines of the locust we actually recorded the conditions in the form of fractions. But in the case of a hook or an antennal or a tarsal segment it is a unit or nothing. To our mind the distinction between substantive and meristic variation is not at all equivalent to a distinction between continuous and discontinuous variation. It is a distinction between two categories of variation only in that one category includes such conditions as permit more readily of extremely slight, nearly insensible, practically unmeasurable differences, as those of pattern or shape or extent, while the other category includes particularly conditions in which any variation must of necessity be fairly obvious, and usually capable of numerical expression.

But we believe, nevertheless, that discontinuous variations occur among insects and that examples of them are presented in the data referring to the species studied by us. For example the occurrence of interpolated, wholly new, and complete cells (determined by the presence of new cross veins or branches of longitudinal veins) in the fore and hind wings of drone honey-

bees (p. 214) and the occurrence of the curious malformations of venation called by us "deformation" (p. 219) among drone bees must be looked on as sports or truly discontinuous variations. The regular occurrence of a 4-segmented foot, perfectly complete, functional in those numerous specimens of Blattidae (p. 296) in which natural regeneration has taken place, may be looked on as an example of discontinuous variation. Although no difference in tarsal segments less than that of one is conceivable, it is quite conceivable that the foot with one fewer than the normal number might be in such condition that it would be obviously a 5-segmented foot with one segment dropped out; in other words that when compared with a normal 5-segmented foot it would appear to be a modification of such a foot with some one segment—and that readily determinable—wanting. But that condition is not at all what appears after the cockroach regenerates a foot. The new foot is only very little, if any, shorter than the normal 5-segmented foot; one cannot say that it is precisely this or that segment which is lost. It is a new kind of foot, apparently just as capable, as "fit," as useful as the 5-segmented kind. We have regularly occurring, in these cases of regeneration, the development of a wholly changed organ, similar as a whole to the old one, but different from it in all its parts, this difference not being one of incompleteness or serial addition or subtraction, but the difference of newness. It is the regenerative mutation of an organ!

The Rigor of Natural Selection and Determinate Variation.—The theory of determinate variation is based on the hypothesis that fluctuating variations are not in all cases, nor necessarily in any case, purely fortuitous and scattering but that because of some intrinsic or extrinsic influence they tend to occur along definite or determined lines. The need for the theory rests on the claimed inadequacy of slight fortuitous variation in offering selection a sufficient "handle" for action. The greatest logical difficulty with the theory is that none of the influences, which are known or may be conceived of, is adequate to cause such an effect as that of producing persistent determinate variations. In the case of any developing individual, determinate

variation can be attained by controlling the environment (kind and quantity of food, degree of temperature, humidity, light, etc.), but if such variations (modifications) acquired during development are not inherited, there will be no advance generation after generation along any certain line. There will be no cumulative effect of such determinate variation. The constant repetition of a certain environment on generation after generation of a certain species would of course produce a constant repetition of certain individual modifications (orthoplacy), but we do not know as yet of any actual effect on the species of such persistent ontogenetic variations.

The need, however, for some such factor in species-forming as determinate variation is obvious and strongly felt. There are certainly few selectionists left who honestly believe that the minute fluctuating variations in pattern, in size, in curve of a vein, in length of a hair, etc., have that life and death value which is the sole sort of value that an "advantageous variation" must have to be a serviceable handle for the action of natural selection. As a matter of fact, no systematist will have escaped having had it distinctly impressed on him that he recognizes differences in the pattern of lady-bird beetles, in the number of fin rays in fishes, in the branching of a vein in flies' wings, that no enemy, no agent of natural selection, can recognize, at least to the extent of pronouncing sentence of death (or not pronouncing it) on its basis. And further, no biologist really satisfies himself with the worn statement, "We must not presume to judge the value of these trivial, these microscopic differences, for we do not know all the complex interrelation and interaction of the organism and its environment." We do not, but we do know for many cases that such differences are actually not of life and death selective value, and reasoning compels us to believe to a moral certainty that in other cases these fortuitous trivialities have similar lack of life and death importance. The case of the variation of the convergent lady-bird beetle, *Hippodamia convergens* (p. 257 et seq.) is distinctly in point. In our account of this variation we have called attention to the suggestiveness, in its light on the rigor of the "struggle for existence" among individuals, of the fact that

among several thousand individuals, gathered together to hibernate after an active life, having been exposed to the attacks of bird and insect enemies, to the rigors of climatic conditions and to the necessities of obtaining food (other smaller insects, as aphids, etc., caught alive), such a range of variation in pattern is found as enables us to describe (so that they may be actually readily distinguished by verbal description), eighty-four "aberrations" or pattern-variates: lady-birds with no spots, with one, with two, with three, with each of all the numbers up to and including eighteen distinct small black spots, the different numbers usually being represented by several different combinations of spots. Systematic entomologists describe *Hippodamia convergens* as a brown-red beetle with six black spots on each elytron and this description is true for most beetles of this species. But not at all for all; nor even approximately for many. After a season of exposure to the struggle for existence, to the rigors of selection, individuals with one spot, with six spots, with twelve spots, with eighteen, find themselves alive and healthy; they come together to pass a quiet winter under the fallen oak leaves on a mountain side ready to mate miscellaneous in the spring and produce young of all manner of pattern (as far as number and arrangement of spots go) which young, whether twelve-spotted as they ought to be, or no-spotted, or eighteen-spotted as they may be, will apparently go safely through life despite the malvolent search of the all-powerful bug-a-boo, Rigor of Selection!

Directly touching the point, too, are our data of the variation of series of honey-bees collected from free-flying individuals after exposure as adults to the rigors of out-door life, as compared with the variation in the series of bees, adult, but collected just as issuing from the cells before being exposed as adults in any way to the external dangers of living. Series of both drones and workers representing both exposed and unexposed individuals were studied. The results of this examination are, put in one statement, that the variation among the exposed individuals is no less than that among the unexposed individuals. This means that these various mostly slight blastogenic variations (although in such important organs as the wings) which occur among bees at the time of their issuance as active,

winged creatures, are not of sufficient advantage or disadvantage to the individuals to lead to a weeding out (by death) or saving of such varying individuals by immediate selective action. Whatever the rigor and danger of the out-doors bee life, these variations seem to be insufficient to cut any figure in the persistence or non-persistence of any individual in the face of this rigor.

Still other cases in point are those revealed by our study of the variation in the pattern of various insects with incomplete metamorphosis, as the leaf-hopper *Tettigonia* sp. (p. 287), the Capsid flower-bug, (p. 291), the water-boatman *Corispa* sp. (p. 293) and the variation in structure of other insects with incomplete matamorphosis, as the variation in number of tibial spines of the red-legged locust *Melanoplus femur-rubrum* (p. 301), in the periodical cicada, *Cicada septendecim* (p. 306), etc. In all these cases variation of much range and variety is found in series of the adult individuals, during which a more or less protracted post-embryonic development have been exposed to the struggle for existence, with their patterns and superficial structural characteristics in practically the same conditions as found in the adult stage. This variation has existed for the most part, *all through the exposed life of the individual*, and has had its chance to influence for weal or woe the fate of the individual. How much influence have these variations exerted?

Our case which most nearly seems to illustrate determinate variation is that of the variation of the flower-beetle, *Diabrotica soror* (p. 274 et seq.). Among a thousand individuals collected on the university campus in 1895, a certain condition of variation in the elytral pattern exists as represented graphically by figure 53. In 1901 and 1902, other thousands collected from the same place and examined to determine the condition of the variation in this pattern show a distinctly different status, as illustrated in figures 51 and 52. (To be sure that a series of 1,000 individuals really reveals the conditions of this pattern variation, repeated series of 1,000 individuals each were examined and found practically identical.) The difference in the variation status between the 1895 lot and the 1901-1902 lots consists in the dominance in 1901-1902 of one of the two

modal conditions found to exist in the species, which in 1895 was not the dominant one. There has been a marked change in seven years, not in the pattern itself but in the prevalence or dominance of one type of pattern.¹ Has the change been brought about by natural selection? Or is it the result of a determinate variation caused by we know not what intrinsic or extrinsic factors? The variation in *Diabrotica*'s elytral pattern is wholly comparable with the variation in *Hippodamia*'s elytral pattern. The fusion, partial or complete, of two adjacent spots produces *Diabrotica*'s variety of pattern; the suppression or addition, partial or complete, of various spots produces *Hippodamia*'s larger variety. But in *Hippodamia* all the variety exists among individuals after exposure, for practically all of the time that such exposure, will occur, to the rigor of selection among individuals. Shall any greater effectiveness be ascribed to this rigor in the case of *Diabrotica* than actually exists in the case of *Hippodamia*?

When we straighten up after a careful microscopic examination of the pattern of *Diabrotica* to determine its variation, we assure ourselves that no other enemy of these flower-beetles can be conceived to use such discrimination as ours. Does the fly-catcher swooping from its station on fence post or tree branch determine which of two heavily flying *Diabroticas* shall be its prey on the basis of "two middle spots on left elytron partially fused" in one and "these two spots not touching" in the other? To our minds the change in variation status, the dominance of one mode to-day which was the subordinate mode in 1895, is not due to the action of selection. We do not, indeed, hesitate to believe in those "unknown factors in evolution" which may produce among other results that condition of affairs best named "determinate variation." This variation is not necessarily to be conceived of as purposeful or even advantageous; if by its cumulation it becomes a disadvantage of life and death value natural selection, which is after all a logical necessity and un-

¹ Moreover, in a 1904 lot, consisting of the same number of individuals and collected from the same locality as the lot of 1895 and 1901-02, there is (within 2 years) a marked rise in the percentage of the class which, being the mode in 1901-02, was in the minority in 1895.

doubtedly an actual actively-regulative factor in species control, will take care of it.

Variation in Parthenogenetically Produced Individuals and in those of Bisexual Parentage.—Among the “explanations” of variation, that emphasized by Weismann is the most conspicuous. The admixture of the heredity-bearing germ-plasm of two individuals explains why there is variation, and has indeed for chief *raison d'être* (if “rejuvenescence” be not the primary reason) the production of those variations necessary for the grounding of the natural selection theory. Sex is indeed for the sake of variation; variation is the result of amphimixis.

As a matter of fact, parthenogenetically produced animals vary, and by casual inspection seem to vary in practically equal degree with those of biparental ancestry. That in certain instances they really do vary quite as much as do the progeny of two parents is shown by our statistical study of the variation in series of drone honey-bees (parthenogenetically produced) as compared with the variation of the same organs in series of worker honey-bees, of the same maternal parentage as the drones, but having an added parent, with series of workers and of entirely distinct parentage. The organs examined for variation in these series of bees are the wings, organs used by both drones and workers and having no immediate relation either structurally or physiologically to the differentiation of these two castes or kinds of individuals of the honey-bee species. The workers are “incomplete” only in that most of them are infertile: in no other structural or physiological feature of their make-up are they less “complete” than the drones. They are indeed distinctly the more specialized kind of individual of the two and according to one of the early Darwinian canons of variation might be expected on that account to vary more than the drones. But the drones are males and according to another commonly accepted belief, this is the explanation for a larger variation on their part, if such larger variation occurs. As a matter of fact it does. Reference to our account (p. 214, et seq.) shows that the drones in all the series studied show markedly more variation in the venation of the wings (something the entomological systematists expect to see little of, as witness the constant use

of venational characters in keys to families and genera in almost all insect orders) than do the workers, while they show quite as much variation as the workers in the number of the hooks which hold the two wings together in flight. Both these characters, *i. e.*, wing-venation and wing-hooks, are not so-called "male characters"; they are not to be compared with those secondary sexual characters such as ornamental or aggressive spines, horns, patterns, etc., which are the characteristics that give males their special name for ultra-variation.

Moreover we have been able to compare the variation in identical organs, *viz.*, wings in the male honey-bees (parthenogenetically produced) and in male ants (of bisexual parentage) and in all the characteristics studied the male bees varied more than the male ants. Our results stated simply are that in the case of one kind of insect, produced parthenogenetically, variation is quite as pronounced as in two other insects of similar general character but of bisexual parentage.

Variations in Males and Females.—The common belief is that males vary more than females. We do not know on just what evidence, if any, this belief is based, except that derived from an examination of those ill-understood and superficial structures familiarly known as secondary sexual characters, such as ornamental combs, wattles, feather-tufts and color-patterns, and spines, horns and spurs for fighting. The only cases in our series of insects studied which have given us evidence touching this point are those of the honey-bees and mosquitoes. In both these cases we have noted the variation in certain structural characters common to both males and females and distinctly not of secondary sexual character. The result is that we find a larger variation in wing characters in male honey-bees (drones) than in (infertile) female bees (workers), while in mosquitoes we find (using confessedly dangerously short series) that the females show a slightly larger variability. In the case of the bees, we have the complication of parthenogenetic birth for the males.

Correlated Variation; Bilateral Symmetry, Metamerism, Other Correlations.—Insects are bilaterally symmetrical and metameric animals. There are thus right and left and fore and

aft structural correlations. Do the variations, continuous and discontinuous, show similar bilateral and metamerie correlation? Evidence regarding this question will be found on many pages in the present paper, right and left correlation, at least, having been considered and briefly discussed in connection with almost all of the various cases studied. And the evidence is curiously conflicting. For example in the male black ant in which was studied the variations of the venation and number of hooks, a close correlation in the variation conditons of right and left wings exists. On the other hand in the honey-bee the bilateral correlation of variation seems surprisingly small (see pp. 214-222.) In the case of variations in pattern also there is no uniformity among the various cases studied. In *Hippodamia convergens* (p. 257 et seq.) the two elytra show pattern-variations quite independently; in *Diabrotica soror* (p. 274 et seq.) on the contrary there seems to be a marked right and left correlation in the elytral pattern-variation. In the cases of the variation in number of tibial spines on the right and left hind tibiæ of locusts (p. 301) and cicadas (p. 306) we have simply made a brief statement, in each case, of the actual conditions of correlation leaving the reader to draw his own conclusions. In the case of the variation in actual and relative length of the antennal segments of the scale insect, *Ceroputo yuccæ* (?) (p. 310) there is a surprising lack of correlation between the right and left antennæ.

We have not attempted to determine the mathematical expression (coefficient of correlation) for any of the cases studied. The data presented, however, will enable any biometrician who sees an advantage in doing this, to do it. But without checking our results by the use of that method there seems, on the whole, to be a surprising lack of that fine degree of correlation in variation which we should expect to find existing—if we believe that the actual existing conditions of structure and pattern in these bilaterally symmetrical animals are an expression of the result of the action of a rigorous natural selection. If one condition of pattern or structure is the most advantageous (of the many conditions which selection among a host of fluctuating variations could have established) surely this condition

ought to be pretty closely similar on both sides of the insect. That as much bilateral variety as actually exists, in many of the species examined by us, should exist — a variety comparable in certain cases even with the degree of variety revealed by the comparison of considerable series of individuals — is a state of affairs that only confirms us in the belief that these innumerable small continuous variations, on which for so long the thorough-going selectionists have put their faith as the sufficient bases for natural selection's species-forming work, are clearly not competent to serve as such bases. If these "continuous" variations are the foundation stones of new species, some other agent than selection must be found or invoked to build several courses on them, to produce some cumulation of them, before natural selection finds them of that life and death worth which is the prerequisite for her potent interference.

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